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Lifetime of Human Visual Sensory Memory: Properties and Neural Substrate

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To identify the neural substrate of VSM, the lifetime for the decay of the neural activation trace in the human primary visual cortex (area V1) were deduced from the visually evoked potential (VEP) recordings for each subject. There was a precise match between the V1 lifetime and the VSM lifetime for each subject. The match even held when both psychophysical and physiological lifetimes were prolonged by practice, or shortened by enhancing the mean luminance of the stimuli above the background. This precise match indicates that the cortical location for VSM is V1.

Comments
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LIFETIME OF HUMAN VISUAL SENSORY MEMORY:

PROPERTIES AND NEURAL SUBSTRATE

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Approved: _____

To my father: Qingyu Yang (1933-1980),

who devoted his life to his dream that his sons go to college

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Abstract

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To identify the neural substrate of VSM, the lifetime for the decay of the neural activation trace in the human primary visual cortex (area V1) were deduced from the visually evoked potential (VEP) recordings for each subject. There was a precise match between the V1 lifetime and the VSM lifetime for each subject. The match even held when both psychophysical and physiological lifetimes were prolonged by practice, or shortened by enhancing the mean luminance of the stimuli above the background. This precise match indicates that the cortical location for VSM is V1.

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CHAPTER 1. A REVIEW OF VSM STUDIES IN PARTIAL-REPORT PARADIGM

Psychophysical studies of visual sensory memory (VSM) have been extremely controversial. This is evidenced by inconsistent results and competing models. Consequently, the properties and neural substrate of VSM have remained ambiguous. The goals of this project were to accurately measure the time course of the VSM decay, characterize the properties of VSM and identify its neural substrate. To lay the foundation for an accurate measurement of VSM lifetime in this study, this chapter reviewed the literature to identify the problems in previous VSM studies.

This review was focused on the VSM studies based on the partial-report paradigm developed by Sperling (1960). Sperling's paradigm was chosen because (1) it was the first paradigm in modern cognitive psychology to reveal and define VSM and (2) it has been most extensively studied.

The review started with Sperling's 1960 study and his classic model for partial-report performance (Sperling, 1967). Then several challenges to the classical concept of VSM as an icon were outlined. The challenge having the strongest impact was in Coltheart's (1980) tutorial review, in which he argued that iconic memory is not *visible persistence*, but an invisible and postcategorical information persistence. Alternative models for partial-report performance following his arguments were described, and the current status of studies on VSM was summarized. Finally, the problems that caused these controversies were identified.

1.1 The Classic Concept of Visual Sensory Memory

It has been recognized since Aristotle (384 -322 B. C.) that a vivid memory persists briefly after the termination of a visual stimulus. Its physiological basis and phenomenal consequences have long been debated (for reviews, see Allen, 1926 and Boynton, 1972). Modern cognitive studies of this phenomenon were ignited by Sperling's elegant demonstration of such transient vivid visual memory with his partial-report procedure (Sperling, 1960).

1.1.1 Sperling's Partial-Report Study

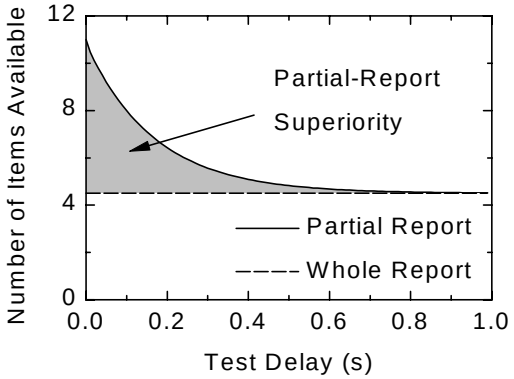

Figure 1.1. Illustration of the basic results in Sperling (1960). The shaded area, the partial-report superiority, reveals the decay of VSM. The area below the dashed line represents the contribution of the durable memory.

In his 1960 experiment, Sperling displayed a set of letters arranged in a 3 x 4 matrix for 50 ms. In the partial-report condition, a tone was delivered after a delay to indicate a row to report. In the whole-report condition, subjects were instructed to report as much as they can from the whole display. The performance was measured by the

number of items available at various test delays. Performances for these two conditions are illustrated in Figure 1.1.

The main finding was that partial-report performance rapidly decreases within a fraction of a second and falls to the asymptotic level of about 4.5 items. The asymptote was equivalent to the whole-report performance level. The number of items reported in the whole-report condition was independent of the test delay. The difference between partial-report performance at shorter time delays and its asymptotic level performance at longer time delays was called the partial-report superiority (the shaded area in Figure 1.1). This difference was thought to reveal the "visual information store" (Sperling, 1960) or "iconic memory" (Neisser, 1967). In Sperling's experiment, the time course of VSM was roughly 0.25 s.

1.1.2 The Classic Concept of Visual Sensory Memory: Iconic Memory

The studies of VSM in the 60s' and 70's characterized VSM as a transient, visible, precategorical, high-capacity visual icon. It registers incoming visual information for further processing by other components of the information processing system (Coltheart, Lea, & Thompson, 1974; Dick, 1974; Von Wright, 1972). It was thought of as a sensory buffer in the visual modality in most of the models of human information processing (e.g. Atkinson & Shiffrin, 1968; Haber, 1969; Lindsay & Norman, 1977, pp.310-315; Neisser, 1967, chapter 2; Sperling, 1960).

Although the locus of VSM in the visual pathway was not specified, the idea of a passive, large-capacity, and rapidly decaying central store pointed to the early visual sensory cortical areas.

1.1.3 Classic Two-Memory Model for Partial-Report Performance

As illustrated in Figure 1.1, performance in the whole-report task was constant at all test delays (Averbach & Sperling, 1961; Dick, 1967; Sperling, 1960) and was not affected by a post-stimulus mask (Averbach & Sperling, 1961; Sperling, 1960, 1963). By contrast, the partial-report superiority was maskable. The whole-repot performance and the long-lasting asymptotic level of partial-report performance were thought to be supported by a postcategorical durable memory which has limited-capacity (see, for example, Coltheart 1972, 1977; Sperling 1967). Thus, according to the classic account for partial-report performance, partial-report performance is jointly supported by two memories: the initial rapid decaying, precategorical, large-capacity VSM, and a sustained, postcategorical, limited-capacity durable memory. In addition, in the serial comparison paradigm (Philips, 1974), the performance at the short test delays was maskable and was considered as a VSM component. He also found that a slight shift of the retinal location of the two sequential stimuli decrements the performance at these short delays. This suggests that VSM is retinotopic, with durable memory being spatiotopic

According to Sperling's model (1967), the visual pattern first enters the VSM. The information in VSM is rapidly scanned (1 item / 10 ms) into a recognition buffer

where it is maintained for retrieval. At short test delays where VSM is available, the subject can selectively scan the cued items for insertion into later stages of the processor for subsequent report. For longer test delays when the VSM is gone, the subject retrieves information from the durable, limited-capacity storage for report. This model represents the classical explanation for the performance in the partial-report paradigm (e.g. Coltheart, 1977).

These two memory components in partial-report performance exhibited different time courses. VSM has a time-course of about 0.2 - 0.3 s. By contrast, the second memory is durable. In the early partial-report studies subjects were able to maintain the durable memory with full capacity of about 4 items for a few seconds. However, the durable memory could decay to a lower level after a second or two if subjects are distracted by a concurrent task (Sakitt & Appelman, 1978). The time course for the decay of this durable memory has been shown to be a few seconds in a serial comparison paradigm by Philips (1974, 1983). Cowan (1995) also speculated that it has a half-life of 2-4 seconds.

1.1.4 The Unitary Persistence Hypothesis

Sperling's study stimulated considerable interest in VSM. Several alternative procedures were developed to directly measure the duration of the VSM (see, Coltheart, 1980; Long, 1980, for reviews). These procedures were thought to measure the different aspects of the same visual persistence. This was called the *unitary persistence hypothesis* (Weichselgartner & Sperling, 1995).

However, there have been many discrepancies between the estimates of the time course for VSM. These discrepancies are probably caused by the differences in stimulus parameters and task requirements. In addition, these discrepancies might be caused by specific systematic biases in the procedures. In other words, VSM might play a dominant role in these tasks, but the procedures may not have been optimized to measure the time course of VSM. A critical review of the problems for an accurate measure of VSM in various procedures was provided by Long (1980).

Hawkins and Shulman (1979) recognized that the duration of a stimulus could be estimated as the period between the sensation of the stimulus onset to the sensation of the beginning of the disappearance or, alternatively, to the end of the disappearance. These two subjective durations minus the real stimulus duration resulted in the Type I and Type II persistences suggested by Hawkins and Shulman (1979). Although the exact mechanism of detecting the stimulus offset was controversial (Di Lollo, 1984; Long, 1979), such a categorization of the two types of measurements suggested that these different procedures measure the same sensory residual, not two different types of residuals. Di Lollo (1984) noted that the above Type I and Type II persistences have also been interpreted with little or no additional justification, as referring to different types of persistence, each with different mechanisms.

1.2 Challenges to the Classic Concept of VSM

The studies with partial-report procedure had soon become a primary paradigm in cognitive studies of human information processing. However, the partial-report task is

difficult for the subjects perform and many studies found little or no partial-report superiority effects. Consequently, inconsistent results emerged and the properties of VSM have been controversial. The classic concept of VSM described above has been challenged in several ways.

1.2.1 Does Partial-Report Superiority Reveal Iconic Memory?

In a series of papers, Holding (1970, 71,72,73) challenged the iconic memory paradigm by citing the failures to obtain the partial-report superiority. He suggested that the partial-report superiority was due to some artifacts, such as guessing and response selection. Von Wright (1972) and Dick (1974) clarified this issue by specifying the conditions where the partial-report superiority is obtained and where it is not. This challenge was also systematically defended by Coltheart (Coltheart, et. al, 1974; 1980). In general, the failures to obtain partial-report superiority were caused by output interference, using an ineffective cue, or using a small number of items in the display that did not overload the short-term memory system. Coltheart et al (1974) concluded that the iconic memory concept is necessary to account for the partial-superiority effect.

1.2.2 Is the Icon a Central Cortical Effect?

The classic concept of iconic memory implies that the early visual cortex is the location of the icon in the visual pathway. Sakitt and Long proposed that iconic memory is a retinal afterimage effect. Their studies (e.g., Long, 1982; Long & Beaton, 1982; Sakitt & Long, 1978, 1979) revealed that the partial-report superiority effect is enhanced by increases in stimulus duration and intensity. These properties simulated those of the

retinal afterimage (Brown, 1975). However, they used dark-adapted subjects with relatively bright, large-sized stimuli on a dark or very low luminance background which favor the production of a retinal afterimage.

The studies of Sakitt and Long indicated that an afterimage could produce the partial-report superiority. Nevertheless, there are circumstances where the partial-report superiority can be observed without afterimages (Breitmeyer, 1984). Therefore, afterimages are not necessary for the partial-report superiority to occur. The notion that the retinal afterimage accounts for iconic memory cannot be generalized to typical visual conditions. As Breitmeyer (1984) stated, "This should not be taken to imply that photoreceptor persistence is the source of visible persistence. Rather it suggests that photoreceptor persistence is a source of neural persistence; and, hence, one possible precursor of visible persistence"(p. 86). Thus a cortical source account for iconic memory (defined here as visible persistence) is implied in various psychophysical studies (for a review see, Breitmeyer, 1984, p. 87-94). No experiment has provided direct evidence for the cortical source of iconic memory.

1.2.3 Is Iconic Memory a Necessary Concept?

Haber (1983) introduced a controversial argument against the iconic memory paradigm. His basic argument was that because the icon plays no role in visual perception outside the laboratory, it is not necessary to propose such an idea. However, 30 out of 32 commentaries took issue with Haber's position (Haber, 1983).

1.2.4 Is Iconic Memory Visible Persistence?

The most severe challenge to the classic concept of VSM as the icon was from Coltheart (1980), and the issues he raised have yet to be settled. Based on his review of the literature, Coltheart concluded that the duration of the visible persistence measured by a variety of techniques exhibit a dual-inverse effect: an *inverse duration effect* (the longer the stimulus lasts, the shorter is its persistence after stimulus offset) and an *inverse intensity effect* (the more intense the stimuli, the shorter its persistence). By contrast, the duration of iconic memory measured by the partial-report superiority did not show such dual-inverse effect. Based on this observation, Coltheart augured that iconic memory cannot be identified with visible persistence because they show different functional properties. He suggested that the partial-report procedure measures information persistence which is nonvisible and postcategorical.

Although not everyone agrees with Coltheart (e.g. Long, 1980), his review had a substantial influence on the theories of iconic memory. Most scholars in the field of vision believe that there is no unitary "iconic memory", but rather that there is a variety of visual memories in the early visual processing stages.

1.3 Models for Partial-Report Performance after Coltheart's Review

All of the models for partial-report performance after Coltheart (1980) were based on the notion that iconic memory revealed by partial-report superiority differs from visible persistence. As discussed earlier, partial-report performance reveals an initial transient memory and a more durable memory. These subsequent models also contain

two or three components to account for partial-report performance. Another feature of these models is that they have mainly focused on accounting for the observation that most errors in the partial-report task are location errors rather than item intrusion errors (e.g. Dick, 1969; Townsend, 1973). This observation was also taken as evidence for the argument that the partial-report task taps a postcategorical storage in which items from the display are identified and well remembered, but their locations are forgotten (e.g. Irwin & Yeomans, 1986).

1.3.1 The Dual-Buffer Model

This model was developed by Mewhort and co-workers (Campbell & Mewhort, 1980; Mewhort, Campbell, Marchetti, & Campbell, 1981; Mewhort, Marchetti, Gurnsey, & Campbell, 1984). According to this model, information from a letter display is first stored in a raw, precategorical form in a feature buffer, and is transformed to an abstract, postcategorical representation that is stored in a character buffer, which will also preserve the relative spatial positions of items in the display.

1.3.2 Irwin's Two-Component Model

Another model was proposed by Irwin and his co-workers (Irwin & Brown, 1987; Irwin & Yeomans, 1986; Yeomans & Irwin, 1985). In his initial model (e.g., Irwin & Yeomans, 1986), the nonvisible information persistence has two components: (1) a visual analog representation of the display which contains form and location information of the display; it is maskable and decays rapidly within 0.1 to 0.3 s after the offset; and (2) a durable, nonvisual identity representation which is not maskable by perceptual masks and

contains less accurate spatial information. The latter component was subsequently updated to be a location-specific, limited capacity memory (Irwin & Brown, 1987).

These two models are very similar and only differ in some details. For example, the latter model assumes that the selection occurs from a precategorical, maskable, duration-independent representation, rather than from a duration-dependent postcategorical representation. They also have different mechanisms for error patterns and the effect of a mask stimulus.

1.3.3 Di Lollo's Three-Component Model

Not all the models exclude visible persistence from partial-report performance. Di Lollo and Dixon (1988; Dixon & Di Lollo, 1991) proposed that the initial rapid decaying memory which maintains spatial information is determined jointly by two components. One is the schematic persistence which is postcategorical and is time locked to the stimulus offset. The other is the visible persistence which is precategorical and is time-locked to the onset of the stimulus. The asymptotic performance was attributed to a verbal short-term memory which corresponds to the durable memory of Coltheart (1977, 1980). In this model, there are at least three memories involved in the partial-report task. By incorporating three memory components, they were able to account for the intensity and duration effect they observed with partial-report procedures.

However, there is no direct evidence for the idea that schematic memory decay is involved in the partial-report superiority effect. In addition, this model predicts that for long stimulus durations (e.g. > 200 ms), the partial-report superiority effect will be

caused by only the schematic memory decay and will be not affected by stimulus intensity and duration. Such predictions need to be explicitly tested.

1.3.4 How Far Have These Models Progressed?

Interestingly, the theoretical developments following Coltheart's arguments did not proceed beyond the classical models for partial-report performance. As Irwin and Brown (1987) noted, "…it is interesting that this modification, which posits a precategorical visual representation feed into an abstract, limited capacity representation, is very similar to the traditional notion of an iconic memory which feeds into short-term memory. The major difference is that the information in the precategorical representation of Irwin and Yeomans is hypothesized to be nonvisible. Nonetheless, it would be ironic if a slightly-modified version of the traditional theory turned out to be correct after all these years" (p.337). Even the last modification may not be necessary because whether visible persistence is involved in partial-report performance is still an open question. Thus, the development of the theories intended to substitute the classic two-memory model for partial-report performance (e.g. Coltheart, 1972; Sperling, 1967) turned out to approach the two-memory model. This circular theorizing represents the chaotic status in this area and raises doubts about Coltheart's arguments.

1.4 Current Status of Visual Sensory Memory Research

Although the classic concept of VSM as iconic memory has been challenged and the concept of VSM has changed over the years (e.g. Cowan, 1995), the basic finding of Sperling's experiment and the classical account are widely accepted in cognitive

psychology and are taught in most textbooks of cognition. However, due to inconsistent results and unsettled theoretical issues, the VSM studies which used to be emphasized in the early days of cognitive psychology have recently become quiet recently. Another reason for this situation was according to Cowan (1995), a shift of interest to the higher-level semantic and lexical representations due to the development of new experimental procedures such as priming.

The controversial situation in VSM studies has severely hindered the application of the paradigm for assessing individual performance and investigating its neural substrate. Given the recent expansion of our understanding of information processing in the visual pathways, our understanding about the neural substrate of VSM is embarrassingly limited. Why is the neural substrate for VSM interesting? One reason is that it is a vivid form of awareness, as Crick and Koch (1990) noted. The identification of the neural substrate of VSM might help to open a window to the neural substrate for human consciousness.

To conclude, it is worth citing an observation by Cowan (1995) on the current status of sensory memory in general: "…the research on sensory memory has reached a plateau at which it is difficult to know how to proceed. Although much has been learned and important questions remain, a muddle of alternative methods exists, each with accompanying methodological concerns" (p. 51).

1.5 Causes of the Controversies about the Concept of VSM

The classic concept of VSM as a transient, precategorical, large-capacity visible persistence has been widely accepted in cognitive psychology, but it is largely controversial among the researchers in VSM studies. It seems that there are evidence against this concept of VSM, but none is sufficient to prove that it is wrong. The study of VSM is full of inconsistent results and controversial theories regarding the properties of VSM. This merits a survey of the literature to identify the problems that caused the confusion so that they could be avoided. My literature survey identified three causes for the confusions in the study of VSM.

1.5.1 Problem 1: Difficulties with the Partial-Report Task

Sperling's partial-report procedure is not an easy task for naïve subjects. It is easy to understand but not easy to perform, as pointed out by Long (1985). Thus, some studies reported no partial-report superiority effect (Eriksen & Steffy, 1964; Mayzner, et al. 1964) while others reported a lack of partial-report superiority for some subjects (e.g. Appelman, 1980). This led to wide individual differences under identical conditions. Because a monotonic decay is not always observed in individual data, many studies ended by averaging data across large numbers of subjects to obtain a monotonic decay of performance to reveal VSM. Thus, it is difficult for the original partial-report task to accurately characterize the time course of VSM for individual subjects. Averaged data based on large numbers of subjects are not sufficiently sensitive to detect a change in the

time course of VSM. Long (1985) has attributed the lack of sensitivity or temporal resolution of the procedures to the ambiguities of the temporal properties of VSM.

Although a modified version of the partial-report procedure, the bar-probe procedure, has been used in some VSM studies, the accurate characterization of individual VSM lifetimes and illustration of its functional properties have not been achieved.

1.5.2 Problem 2: No Well-defined Measure for the Time Course of VSM

Most studies of VSM or iconic memory with the partial-report procedure have been concerned with its time course, but this time course has not been appropriately characterized. Usually, the time course of VSM decay in the partial-report paradigm is measured to the point where the performance is no longer significantly above the asymptote (Gegenfurtner & Sperling, 1993). Cowan (1995) has pointed out that it is not appropriate to speak of the "duration" of an exponential decay, because in principle it takes an infinitely long period of time to reach the asymptote.

The consequence of the lack of a well-defined measure for the time course of VSM is that its temporal properties have been ambiguous in published studies. Scholars have different opinions regarding how the time course of VSM should be assessed. For example, Keele and Chase (1967) measured partial-report performance with stimuli of three intensity levels. Coltheart (1980) recognized that it is difficult to compare the time courses of VSM for stimuli of different intensity in that study because the icons started to decay from different levels in different conditions. Long (1980) and Nisly and

Wasserman (1989) concluded that there is a positive intensity effect because stronger stimuli led to larger partial-report superiority effect. It has become a routine in this area to assess the time course of VSM by the overall performance or the performance at a specific test delay.

However, higher performance does not necessarily indicate longer persistence because the performance level also depends on the initial and asymptotic levels. The form of VSM decay has been assumed as exponential. For an exponential decay, the appropriate measure for its time course should be the time constant of the exponential function. Unfortunately, the exponential decay of VSM has not been well established.

1.5.3 Problem 3: Identifying Iconic Memory as Partial-Report Performance

Problems 1 & 2 reflected the difficulties in using the partial-report procedure to accurately characterize the time courses of VSM; however, the primary cause for the controversies in VSM studies is a different usage of the term "iconic memory".

Sperling (1960; 1967; Averbach & Sperling, 1961) carefully discriminated the two memory components in the partial-report procedure by attributing the partial-report superiority as a measure of iconic memory and the asymptote of the partial-report or the whole-report performance as a measure of durable memory. Although no explicit method was developed to dissociate these two components from the performance, it was clearly indicated that the partial-report superiority effect, not the overall performance, corresponds to VSM or the iconic memory component. However, most of the published studies based on the partial-report paradigm identified partial-report performance, instead

of the partial-report superiority, as the measure of VSM or iconic memory. The consequence of this is that any change in partial-report performance, including those caused by a change in the durable memory component, has been attributed to iconic memory component. This led to the confusion regarding the properties of VSM when examined with the partial-report paradigm. This will be further illustrated in section 1.6.

Referring to partial-report performance as iconic memory is also common in the theoretical evaluations of the classic concept of iconic memory, which led to the "split of the icon". For example, the abstract of Mewhort et al. (1981) started with the statement, "the partial-report tachistoscopic has been used to define iconic memory, a labile image-like precategorical visual store"(p. 50). Then they summarized their data and stated at the end that "Iconic memory is a construct that oversimplifies the information processing system used in the bar-probe task" (p. 50). Evidently, the authors referred to partial-report performance as "iconic memory" and overlooked the durable memory component. They used their dual-buffer model that contains two memories to explain their data for the different location and intrusion errors in the bar probe performance, and argued that these data cannot be explained by a single icon. Obviously, they assumed that only iconic memory is involved in the bar-probe performance.

In fact, in the first bar-probe study, Averbach and Coriell (1961) recognized that two memory components are involved in the bar-probe task by noting:

> The fact that the measured decay curves do not fall to zero suggests that the measured performance contain components of a more permanent

> memory, as well as the short-term memory components that we would like to measure. In this context, the 25 to 35 per cent final performance level (which represents 4 to 5.6 letters) is attributed to what the subject has read into his more permanent memory (p. 315).

Other lines of theories for the iconic memory (e.g. Di Lollo & Dixon, 1988; Irwin & Yeomans, 1986) also identified partial-report performance as the experimental measure of iconic memory and concluded that the concept of iconic memory is not efficient to account for partial-report performance.

1.6 Confusions about the Properties of VSM

This section examined the controversies regarding the classic concept of VSM to illustrate how the failure of discriminating iconic memory from partial-report performance resulted in confusion about the properties of VSM.

1.6.1 Is VSM Visible Persistence?

Coltheart (1980) challenged the classic idea of VSM as the visible persistence based on his conclusion that the visible persistence shows the dual-inverse effect and the partial-report procedure does not. His argument had a great impact on the subsequent models for partial-report performance. However, this argument is problematic.

First, his conclusion about the dual-inverse effect in visible persistence is problematic. Some scholars (Long, 1980; Nisly & Wasserman, 1989) have questioned his conclusion and pointed out that (1) not all of the measures of visible persistence exhibit the dual inverse effect; and (2) the procedures he considered as measuring visible

persistence might measure different aspects of the persistence such as Type I and Type II defined by Hawkins and Shulman (1979).

Second, the evidence showing a lack of the dual-inverse effects on partial-report performance is rather sparse. The lack of such an effect in these experiments might be due to a small change of energy in the stimuli or lack of sensitivity in the procedure (Long, 1985; Massaro & Loftus, 1997). It was found that under appropriate conditions, there is a robust inverse duration effect in partial-report performance (Di Lollo & Dixon, 1988, 1992; Dixon, 1985; Dixon & Di Lollo, 1991). However, these effects were assessed by comparing the overall performance, which does not necessarily reveal the time course of iconic memory. Thus, effects of the stimulus parameters on the time course of iconic memory remain to be accurately assessed.

Third, Coltheart's direct comparison of the results of the visible persistence and that of the iconic memory studies was problematic, because these experiments differed in procedure and stimulus parameters (Massaro & Loftus, 1996).

Finally, Coltheart did not explain why such information is not used for the partial-report task if subjects see the visual pattern persist for hundreds of milliseconds. One probable explanation is that visible persistence has a shorter lifetime than the nonvisible information persistence. However, no experiment has been done to compare these lifetimes. As pointed out by Pashler & Carrier (1996), the empirical evidence for the existence of a separate identity representation from visible persistence is far from

compelling. There is no direct evidence that visible persistence is not involved in partial-report performance.

The only study that measured both iconic memory and visible persistence in the same experimental condition and for the same subjects was that of Appelman (1980). For visible persistence, he provided a click of 10 ms duration after various delays following a visual display (50 ms) and asked the subjects to report whether the image of the display was still visible at the time of the click. Visible persistence was measured by the probability of saying "yes" as a function of the test delay. Only one of nine subjects showed a monotonic decaying partial-report superiority effect. For this subject, both the partial-report superiority and the probability of responding "yes" in the visible persistence performance reaches zero at the test delay of about 450 ms. Such a similar time course between iconic memory and visible persistence also holds in the averaged data. These data seem to suggest the involvement of visible persistence in the partial-report task. So far, the relation between visible persistence and iconic memory has been primarily discussed on the basis of results from different experiments concerned with other issues. It should be directly assessed in future studies.

1.6.2 Is VSM Precategorical?

In his review, Coltheart (1980) also suggested a postcategorical store as an alternative account for iconic memory. This idea was taken seriously by subsequent theorists. The main evidence was a categorical effect on partial-report performance and the observation of the well-kept identity information in partial-report performance.

According to the classic two-memory model for partial-report performance, partial-report performance is jointly supported by a precategorical iconic memory and a postcategorical durable memory. To attribute a specific effect to iconic memory, one has to make sure that the iconic memory is captured. As Dick (1974) pointed out, to capture the iconic memory one has to overload the perceptual system. The more items in the display, the more partial-report superiority could be obtained.

Moreover, any change in partial-report performance caused by a shift of the asymptote which represents the contribution of durable memory should not be attributed to iconic memory. In practice, a specific effect on iconic memory should be a change of the partial-report superiority effect while the asymptote is maintained stable. A change of performance below the durable memory capacity could not be attributed to iconic memory unless additional validation is provided.

Category effect on partial-report performance. A category effect on partial-report performance refers to the superiority of partial-report performance by category cueing over the whole-report performance. The results of this effect were not consistent in previous studies. Some studies did not obtain such an effect (e.g. Bourne, Dominowski, Loftus, & Healy, 1986; Moates & Schumacher, 1980; Von Wright, 1972), while others did (Dick, 1969; Dixon, 1985; Dixon & Shedden, 1987; Duncan, 1983; Merikle, 1980). In general, there seems to be a small category effect on partial-report performance. An important question arises as to why the effect was small and whether this effect could be attributed to the iconic memory component.

Dick (1969) did not obtain a significant partial-report superiority, and the number of available items was between only two and three. He acknowledged that the category effect "seems to be the result of the short-term storage system and not of the sensory register". The studies by Dixon (1985; Dixon & Shedden, 1987) used 7 items in the display, and the highest number of items available was between 2 and 3. Additional validation is required to attribute to iconic memory the category effect found at the asymptotic performance level.

Duncan (1983) used only six items in the display, and he obtained partial-report superiority of about 1.5 items at best. Merikle (1980) used 8 items in the displays and found partial-report superiority of about 0.5 items. In both experiments, the largest number of available items was no more than 5.5 items. Consequently, the perceptual system in these two experiments was slightly overloaded, and only a small partial-report superiority effect was obtained by perceptual cueing. Such a small effect might well be due to the change of the asymptote that is produced by the effect on the durable memory. This might be the case, because the data in Merikle (1980) show that most of the category effect was the shift of the asymptote, which suggests that such an effect could be mainly from a change in the durable memory.

It must be pointed out that the inference as to whether specific information is processed in the icon by the effectiveness of a specific cue may not be appropriate, as pointed out by several authors (Allport, 1989; Duncan, 1981; Pashler, 1998). It is possible that the category information may not be a good cue, even if the items were

categorized. This is somewhat like the situation where one cannot retrieve a book from a shelf by its contents, although the contents are in the book. Therefore, the absence of partial-report superiority by category cueing cannot be taken as evidence for the argument that categorical information is not in the icon.

Obviously, if category information were contained in the icon, it is difficult to understand that the number of items a subject can recognize after a brief display of multiple items is never above the capacity of durable memory, as we will see in the next section. One might argue that the recognition test is not sensitive enough. A more sensitive procedure to detect residual memory is the priming technique. It has been shown that strongly divided attention can eliminate conceptual priming completely (Mulligan, 1997). Such results imply that if an item in the icon is not selected to be processed into the durable memory system, it may not be perceptually categorized. So far, all of the category effects found in partial-report performance are likely to be in the durable memory system, the evidence of a categorical effect specific to the iconic memory has not been shown.

A similar issue exists in visual search where the visual scene is consistently available. The question is whether the representation in which the search is processed is precategory or postcategory, and evidence for both possibilities exists. Lavie (1995) reviewed such studies and proposed that a critical variable is the perceptual load.

The proposition of the necessity to overload the perceptual system for taping the precategorical sensory system (Dick, 1974; Lavie, 1995) is consistent with the idea that

the output in both partial-report and visual search paradigms is from a postcategorical limited capacity system. When the perceptual load is within the limit, all items are fully processed and a postcategorical effect is shown. When the processing system is overloaded, only a small number of items in the sensory system are further processed, and the rest items, which are seen but not recognized exhibit precategorical properties. Effort is needed to dissociate these two systems and characterize how the large capacity precategorical sensory representation and the limited postcategorical representation system cooperatively operate in various tasks and usual life.

Independent identity and location information in partial-report performance. All of the models developed after Coltheart's argument made a strong distinction between spatial and identity information. The main evidence for this distinction is that the rapid initial decay in partial-report performance is accompanied by an increase of location error while the intrusion error remains relatively constant (e.g. Dick, 1969; Mewhort, Campbell, Marchetti, & Campbell, 1981; Townsend, 1973). These authors concluded that location information is lost before identity information, and it was further argued that the partial-report procedure taps a post categorical store in which items were identified and well kept, but their location information may be forgotten (Irwin & Brown, 1987). Here I will examine whether the data actually support these arguments.

The most frequently cited study for the different spatial and location information decay is Townsend (1973). She compared partial-report performance in a bar probe procedure in two conditions. In the first condition, the subject has to report the item at a

cued location; this task requires both location and identity information about the item. In the second condition, an item was presented and the subject was required to report if it was in the display. The latter task does not require spatial location information about the item. Based on her data, she concluded that identity information in a display was not lost as the test delay in increased, and further concluded that "the decay function found in partial-report experiments using a visual probe result from Ss' inability to retain information about where a letter is relative to a visual probe".

What has been ignored and should be made clear is that the relatively stable identity information is just a small portion of all the items presented. To make this point clear, we can replot the relevant data, the short cue condition in Experiment I and II in Townsend (1973), in terms of the number of items available after correction for chance. The formula for this chance correction is given by:

$$I = [(P - P_c)/(1 - P_c)] \times I_{tot} \qquad (1.1)$$

Where P is the probability of correct, I_{tot} and I are the number of items in the display and the number of items available respectively. P_c is the probability of a correct response by chance. According to this formula, responding at chance level (P_c) corresponds to the condition that no item is available in memory; responding perfectly ($P = 1$) corresponds to the condition that all the items presented are available in memory. The intermediate values of P are linearly scaled between these two extremes.

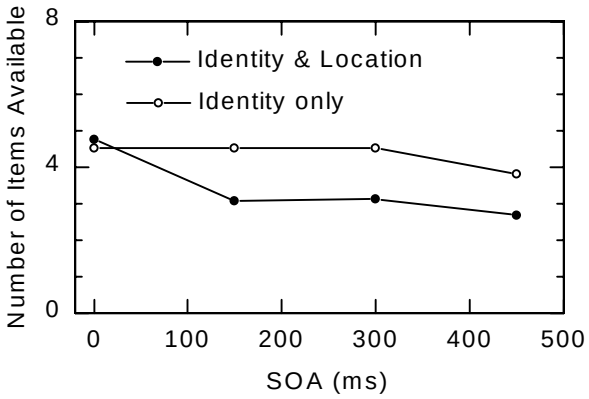

Figure 1.2. Replotting of the results of Townsend (1973). Data were replotted as the number of items available at different SOAs.

Figure 1.2 presents the data after correcting for chance. This figure shows aspects of the results that were not explicit in the original graphs. First, the partial-report superiority effect in the identity & location condition was small; the number of items available at the zero delay was about 4.8, which was slightly above the asymptote. This indicates that the experiment did not catch the iconic memory components well. Second, the difference between these two conditions was much smaller than in the original graphs where the chance was not corrected; the difference was about only 1.5 items for the test delays longer than 150 ms. Such an effect might well be due to the durable memory, because the difference was mainly an asymptote shift. Last, and most strikingly, the number of items available was constantly about 4.5 in the identity-only condition which was exactly the capacity of the durable memory identified by Sperling (Sperling, 1960).

Mewhort & Leppmann (1985) explicitly compared the performance when only identity was tested and the performance when only location was tested. In Experiment I, they presented the subjects with eight-letter string for 50 ms and asked whether a spoken

letter had been presented in the display. In this experiment, only identity information was probed, not location information. In Experiment II, the named letter was always in the display, and the subject was asked to identify its location in the row. This was thought to probe only the location information, but not the identity information. Their data showed that the accuracy was independent of the SOA in Experiment I, but the accuracy dropped rapidly as the SOA increased in the second experiment. They concluded that "subjects lose information needed to locate material in space, not information about identity of the material".

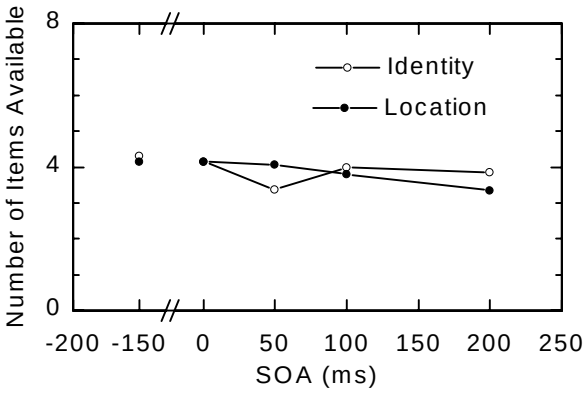

Figure 1.3. Replotting of the results of Mewhort & Leppmann (1985). Data are replotted as number of items available at different SOAs.

Their data were replotted in Figure 1.3 in terms of number of items available after correcting for chance. Again, performance are about the level of the capacity of the durable memory and no partial-report superiority effect was shown. Thus, hardly any property revealed here can be attributed to the icon. What is crucial is that one cannot draw the conclusion from these data that identity information is kept better than location information.

The decrease in partial-report performance accompanied by the loss of location information with increasing test delay was convincing in the data of Dick (1969) and of Mewhort et al. (1981). They also found that when subjects made location errors, they are more likely to report the item next to the probed location than other items. The classic two-memory model for partial-report performance has no trouble with these error patterns. For example, Gegenfurtner and Sperling (1993) suggested that such error patterns could be caused by the fact that when not sure about the right answer, subjects tend to report the items in their short-term memory because it is better to report an item that has been presented than a wild guess.

In conclusion, the above reviewed studies on the categorical effect and on the identity versus location information captured only a very small portion of the partial-report superiority effect, and the small categorical effects obtained could hardly be attributed to iconic memory. Also, there is no explicit evidence in data for a conclusion that identity information is kept better than location information in partial-report performance.

1.6.3 Is VSM Limited in Capacity?

The question of whether iconic memory is limited in capacity has been addressed by examining the effect of concurrent task on partial-report performance. Three studies of this kind arrived at three different conclusions. Doost and Turvey (1971) did not find a significant effect of concurrent task on partial-report performance and concluded that iconic memory is relatively independent of the central processing system. Chow and

Murdock (1975) found a significant effect of concurrent task on partial-report performance at all test delays and concluded that iconic memory is also subject to the limitation of the central processor. Sakitt and Appelman (1978) found that increasing memory load resulted in larger partial-report superiority and they concluded that the partial-report superiority does not imply the existence of an icon.

The results in Doost and Turvey (1971) were consistent with the classic concept of iconic memory that it has large capacity and should not be affected by concurrent task. The majority of the concurrent task on partial-report performance in Chow & Murdock (1975) implies that what was affected is the asymptotic performance, not the time course of the partial-report superiority. Their results may have revealed the effect of concurrent task on the durable memory, not the iconic memory.

Sakitt and Appelman (1978) found that the partial-report superiority effect was increased by adding a concurrent task. The increment of the partial-report superiority effect was however, due to the decrement in the asymptote of the decay measured at the delay of 2 and 5 seconds. This indicates that the durable memory is not maintained at the full capacity for the partial-report task due to the concurrent task. In this case, the partial-superiority effect, which was thought of as the decay of iconic memory, was contaminated by the decay of durable memory.

From the studies reviewed above, we can see that most of the confusion in the experimental studies regarding the properties of iconic memory has been caused by the practice of identifying partial-report performance as iconic memory and ignoring the

contribution of the durable memory to partial-report performance. To assess the properties of iconic memory, it is critical to isolate it from the durable memory which is also involved in partial-report task.

1.7 Conclusions

The early studies on VSM in the partial-report paradigm recognized that both VSM and a durable memory are involved and the VSM component, the icon has been identified as the partial-report superiority effect. The VSM have been characterized as transient, visible, precategorical, and of large capacity. However, due to the difficulties in measuring the partial-superiority effect and the lack of a method to isolate the VSM component from the performance, this classic concept of VSM has been subject to several lines of challenge and the basic properties of VSM have remained largely controversial. In addition to the problems in the measurement, another cause for the confusions of this area is a mistake in the theoretical interpretation of the data -- the identification of partial-report performance as VSM. These problems caused the "splitting of the icon" in the theoretical evaluations of the classical concept of VSM and the misattribution of the properties of the durable memory to the VSM.

The survey of the main evidence against the classic concept of VSM indicates that these data did not disprove the idea that VSM, or iconic memory is visible, precategorical, and of large capacity. To clarify the confusions in this area, we need a more effective procedure to characterize partial-report performance with substantial contribution from VSM component. We also need a mathematical model to isolate the

VSM component form the performance so that properties of VSM can be specifically assessed.

1.8 Goal and Plan of This Study

The primary goal of this study is to identify the neural substrate of VSM by assessing the correlation between the lifetime of VSM and the lifetime of the activation trace in V1. Because the lifetime measurement for VSM has not been well established and its properties have been controversial in the literature, the goal of this study was reached by several steps which determine the global structure of this thesis.

Chapter 1 reviewed the studies of VSM in the context of the partial-report paradigm and identified problems in both the measurement and the theoretical interpretations that led to controversies. This provided a basis for achieving an efficient measurement and clear concept for VSM in this study.

Chapter 2 describes an improved partial-report procedure to achieve an efficient and accurate measure of partial-report performances that contains a substantial VSM component. A mathematical model was introduced to isolate the VSM component from the performance so that its lifetime could be quantified and the properties of VSM could be appropriately assessed.

Chapter 3 contains experiments to characterize the VSM lifetimes for each of a group of subjects. The purpose was to assess whether the VSM lifetime is correlated with V1 lifetime measured later for each of these subjects.

Chapter 4 contains experiments assessing the influences of several stimulus parameters on VSM lifetime to identify the critical parameter that determines VSM lifetime. One motivation was that such variable has not been identified in the literature. Another motivation was to provide information to identify the neural substrate of VSM. To identify a neural activation as the substrate for VSM, it is critical to show that it is sensitive to the same stimulus factor as is the VSM.

Chapter 5 reports experiments to explore the neural substrate of VSM by assessing the correlation between its lifetime and the lifetime of the activation trace in V1 deduced from visually evoked potential (VEP) recordings. Two experiments will assess whether V1 lifetime correlates with VSM lifetime across subjects and whether it is sensitive to the same variable as VSM, respectively.

Chapter 6 summarizes the main results of this study and remarks on the implications of these results on future research.

CHAPTER 2. A NEW PROCEDURE AND MODEL FOR VSM LIFETIME

As discussed in Chapter 1, the classic partial-report task is difficult for subjects to perform and many studies using this procedure obtained either no effect or a small partial-report-superiority effect. Because partial-report-superiority reveals the contribution of VSM to the performance while the asymptotic performance reveals the contribution of the durable memory, partial-report performance with small partial-report superiority effect is dominated by the durable memory. In this case, a change in partial-report performance most likely reveals a change in the durable memory rather than the VSM. To characterize the VSM decay underlying partial-report performance, it is crucial to make the task rely heavily on the VSM to maximize the partial-report superiority effect. It is also necessary to isolate the contributions of the VSM and the durable memory respectively so that the properties of the VSM decay could be specifically characterized. This chapter introduces a new partial-report procedure to produce a partial-report performance having a significant VSM component for individual subjects. It also proposes a model to isolate the underlying VSM component.

2.1 A New Procedure to Characterize Partial-Report Performance

The problems resulting in an inaccurate measurement of VSM decay have been discussed by Long (1980). Here, I shall outline these problems and propose corresponding strategies to avoid them.

Exclusive use of letter or number stimuli. The use of letters or numbers in stimuli automatically triggers categorization and phonological coding. This necessarily

involves the high level processing beyond the sensory representation. Kaufman (1974, p.530) argued that "the fact that linguistic stimuli such as words, letters, and numbers have been the predominating stimuli in the study of information processing is one of the great limitations in this field". Another problem with using symbols in stimuli is that it is difficult to independently manipulate the sensory features (e.g. spatial frequency, contrast, and luminance) as in psychophysical and physiological studies of the temporal properties of the visual sensory system. This made it difficult for the researches in these areas to communicate and the psychophysical studies of VSM have remained isolated from the studies of the temporal properties of the visual pathways.

In this study, a display contained sinusoidal patches arranged in a circle, and a simple feature, the orientation of sinusoidal gratings, was tested. This will presumably make the task more focused on an early visual sensory representation and thereby minimize the involvement of the higher-level symbolic and phonological processing.

Presenting items at different eccentricities. Most partial-report studies presented items in one or several rows. The accuracy for reporting items at different eccentricities exhibits a typical W-shaped pattern. Because visual information at different eccentricities are processed differentially (e.g. Carrasco & Frieder, 1997), averaging data across these items might result in a systematic error in the data. This might reduce the power of the procedure to detect a change in the underlying memories. In this study, the eccentricity of the items are equalized by presenting the items on a circle centered on the

subject's fixation point. This modification was originally proposed by Keele and Chase (1967).

Retrieving multiple items in a trial. In Sperling's partial-report procedure, subjects had to report the items in the cued row which contained 4 items. The performance is subject to output interference. In this study, I shall adopt the modification by Averbach and Coriell (1961) where only one item was probed in a trial.

Verbal response. It was a common practice in partial-report studies to require the subject to verbally report the probed item or items. This led to phonological coding of the items, which result in an additional source of variance. In addition, verbal recording requires an experimenter to write down the subjects' responses, which is not efficient in data recording. In this study, subjects responded by simply pressing one of four keys.

Averaging data across subjects. Most published partial-report studies reported data averaged across subjects. Because different subjects usually show different amount of partial-report superiority effect, the averaged data may contains a large inter-subject variance. In this study, individual data were examined to characterize individual performance. In addition, an assessment session was conducted for each subject before the partial-report test to insure that a partial-report superiority effect will be obtained

2.1.1 Method

Because most experiments of this study involved minor changes of this method, for convenience, the stimuli and procedure described here were called the *standard stimuli* and *standard procedure*, respectively.

Standard stimuli. An IBM-compatible PC with a 14 inch VGA monitor (viewing area 16 cm high by 26 cm width) having a refresh rate of 70 Hz was used to present stimuli and record responses. The monitor was calibrated for gamma correction so that the luminance on the screen is a linear function of the pixel value in the image file. After gamma correction, the pixel value 0 to 255 linearly code the screen luminance from 0 to 40 cd/m^2, thus, the resolution of the luminance control was about 40/256 = 0.16 cd/m^2. The images were made by HIPS, an image generating and processing software under UNIX (Landy, Cohen, Sperling, 1984). The stimulus display is illustrated in Figure 2.1.

With the properties stated in the figure caption, eight spatial configurations of the grating patches were constructed (include the display illustrated in Figure 2.1). The displays were viewed binocularly at a distance of 57 cm, where the visual angle between the center of each patch and the fixation point was 6.5^o, the diameter of each patch was 2.5^o and the spatial frequency of the gratings was 1c/deg.

Long (1985) pointed out that the lack of the dual-inverse effect in the previous partial-report studies might be due to a small change of energy in the stimuli. These studies presented multiple items in or near the fovea and size of each item was small. It is more appropriate to assess the dual-intensity effect with larger items to compare the results with those of the visible persistence studies because the latter generally used stimuli with larger visual angle. In this study, the eccentricity of 6.5^o was a compromise of presenting items of large visual angle and to the fovea as close as possible.

Standard procedure. Subject sat in a quiet, dark room. The test session started after the subject looked at the screen for two minutes to adapt to the background luminance of 20 cd/m^2 on the screen. The subject maintained fixation during the experiment, with a chin-rest to maintain the head position.

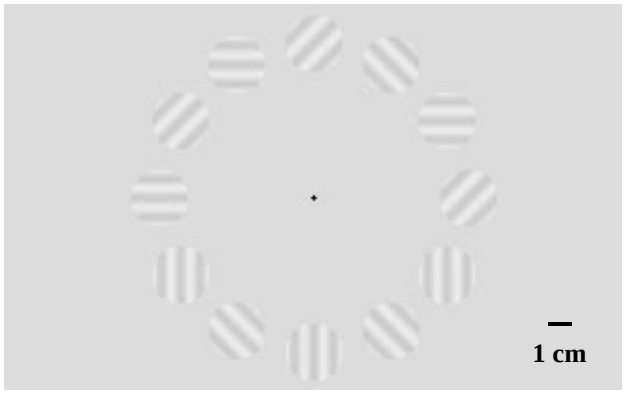

Figure 2.1. An example of the standard visual stimuli. Twelve patches of sinusoidal gratings were equally spaced around a circle surrounding the center of the screen. The four orientations were horizontal, vertical, and 45^o to the left or right of the vertical. Each orientation appeared three times in a display. To avoid perceptual grouping, neighboring patches differed in orientation. The mean luminance of each grating was the same as the background of 20 cd/m^2, and the contrast of the gratings was 20%.

Subject pressed a key to initiate a partial-report test trial. Two seconds after the key pressing, a display as illustrated by Figure 2.1 was presented for 28 ms. After a delay ranging from about 0 to 1.5 sec, a probe bar of 2 cm length pointed from the fixation point to one of the 12 locations where the patches were presented. There were 7 test delays in this standard test. However, the exact number of the test delays and their values might be changed in different experiments for different subjects. The subject pressed one of four keys to indicate the orientation of the indicated patch and had to guess when he or

she was not sure. The subject's response terminated the bar probe and a feedback of either “RIGHT” or “WRONG” was presented 1 cm above the fixation point.

During a test session, each of the 12 locations in each of the 8 displays was tested twice at each of the 7 test delays. Thus a test session contained 12 x 8 x 7 x 2 = 1344 trials. The order of these 1344 trials was determined by a random sequence of the integers from 1 to 1344 generated by random sampling without replacement. A prompt for a short break was presented after every 192 trials. The whole test session was usually completed in 1.5-2 hours.

Before the partial-report test, an assessment session was conducted for each subject. This session was similar to the partial-report test except that the bar was presented right after the display offset with no delay. This session was to make sure that the subject can accurately report the orientation of the indicated patch at zero test delay to insure a substantial decay can be obtained when the test delay is increased. The criterion for passing the assessment was 80% correct in 20 consecutive trials.

2.2 A Model to Isolate VSM from Partial-Report Performance

2.2.1 The descriptive function for partial-report performance

Typical partial-report performance is a decay which asymptotes to an above chance level, and the decay is generally thought to be exponential. The simplest function for such a pattern is:

$$P(t) = A + B\, e^{-t/\tau} \qquad [2.1]$$

where $P(t)$ is the probability of a correct response at test delay t; A, and $B\,e^{-t/\tau}$ characterize the asymptotic performance and partial-report superiority effect respectively. The parameters A, B and τ could be obtained by fitting the data with function [2.1].

2.2.2 A Mathematical Model for partial-report performance

The classic two-memory model proposed that partial-report performance is jointly supported by a constant durable storage and an exponentially decaying VSM (Coltheart, 1972, 1977; Sperling, 1967). In the following modeling, I would follow the classic notion of VSM as iconic memory and these two concepts were used interchangeably in this study. The present task is unlikely to involve phonological processing of the stimuli, and the durable memory is the active maintenance of visual-spatial information for a short period of time before it is discarded. Such memory was characterized by Baddeley and Hitch (1974) as visual working memory or a "visuospatial scratch pad". In this study, the durable memory component is denoted visual working memory (VWM).

To deduce the underlying VSM and VWM from partial-report performance, it is further assumed that these two memories are combined in additive manner. So, if $P_i(t)$ represents the probability of a correct response based on VSM when probed at t after stimulus offset, and $P_w(t)$ represents the probability of a correct response based on the durable memory when probed at t after stimulus offset, then $P'(t)$, the probability of being correct based on either memory when probed at t after display offset is:

$$P'(t) = P_w(t) + P_i(t) - P_w(t)P_i(t) \qquad [2.2]$$

Because it is found in previous experiments that the durable memory is constant across test delays, $P_w(t)$ is independent of time and could be expressed as:

$$P_w(t) = P_w \quad [2.3]$$

The exponential decay of VSM can be expressed as:

$$P_i(t) = P_i e^{-t/\tau} \quad [2.4]$$

Parameter P_i is $P_i(t)|_{t=0}$, and τ is the time constant for the exponential decay of VSM. I define τ as the "lifetime" of VSM. It is the time for VSM to decay to about 1/3 of its original level, because when $t = \tau$, $P_i(\tau) = P_i e^{-\tau/\tau} = P_i e^{-1} = P_i/e \cong P_i/3$.

Function [2.3] and [2.4] with three parameters P_w, P_i, and τ completely describe the VSM and VWM underlying partial-report performance.

The quantitative relation between partial-report performance and the underlying memories could be obtained by taking [2.3] and [2.4], into [2.2]:

$$P'(t) = P_w + P_i e^{-t/\tau} - P_w P_i e^{-t/\tau}$$

$$= P_w + (1 - P_w)P_i e^{-t/\tau} \quad [2.5]$$

Be note that $P(t)$ of [2.1] and $P'(t)$ in [2.5] are the probability of a correct response at test delay of t in the present task before and after correction for chance, respectively.

2.2.3 Deducing the VSM and VWM from partial-report performance

Let us first correct the chance probability for $P(t)$ with:

$$P'(t) = [P(t) - P_c]/(1-P_c) \quad [2.6]$$

Where $P'(t)$ and $P(t)$ are the probability of a correct response with and without correction for chance respectively; $P_c = 0.25$, which is the probability of correct by chance in the present test. Substituting equation [2.1] into this expression and simplify it, we have:

$$P'(t) = (A - P_c)/(1-P_c) + [B/(1-P_c)]\, e^{-t/\tau} \qquad [2.7]$$

Compare equation [2.7] with [2.5], we have:

$$P_w = (A - P_c)/(1-P_c) \qquad [2.8]$$

and $$(1 - P_w)P_i = B/(1-P_c) \qquad [2.9]$$

Take [2.8] into [2.9], we have:

$$P_i = B/(1-A) \qquad [2.10]$$

Equation [2.8] and [2.10] provide the formula to deduce the parameters P_w and P_i for the memories underlying partial-report performance from the parameters A and B for partial-report performance.

These two memories could also be expressed in the terms of number of items available by the following functions:

$$\begin{aligned} I_i(t) &= I_{tot}\, P_i(t) \\ &= I_{tot}\, P_i\, e^{-t/\tau} \\ &= I_{tot}\, [B/(1-A)]\, e^{-t/\tau} \end{aligned} \qquad [2.11]$$

$$\begin{aligned} C_w &= I_{tot}\, P_w(t) \\ &= I_{tot}\, P_w \\ &= I_{tot}\, [(A - P_c)/(1-P_c)] \end{aligned} \qquad [2.12]$$

Here $I_{tot,}$ is the number of items in a display; and I_i, C_w are the number of items available in VSM and VWM, respectively. Parameter C_w is called the capacity of VSM because it is the maximum number of items the subject could fully keep in VWM for a short period. It is the maximum amount of information subject could capture form a brief display and could actively maintain for a short period.

Two conditions must be satisfied to apply the present model to deduce the VSM and VWM components from partial-report performance function. The first is that there must be a partial-report superiority effect. Which is, $B > 0$. If $B = 0$, function [2.9] can not be solved. The second requirement is that partial-report performance must show a stable asymptote to satisfy the assumption that the VWM is constant.

2.2.4 Why It Is Necessary to Overload the Perceptual System to Characterize VSM?

It was discussed in sections 1.6.2 & 1.6.3 that it is critical that the perceptual system be overloaded to reveal the VSM component in the partial-report paradigm. The present model for partial-report performance clearly illustrates this point.

When the number of items in the display equals or is below the capacity of VWM, all the items could be transferred and maintained in VWM for a short period of time. During the period the information in VWM is fully maintained, the probability of a correct response based on VSM, the $P_w(t)$ is 1. So, from [2.2],

$$P'(t) = P_w(t) + P_i(t) - P_w(t)P_i(t)$$

$$= P_w(t) + [1 - P_w(t)]P_i(t)$$

$$= 1 + (1 - 1)P_i(t) = 1$$

In this case, $P'(t)$ is independent of $P_i(t)$, any change in the VSM will not influence partial-report performance. However, it should be careful not to generalize this conclusion to other paradigms. It is possible that when perceptual system is not overloaded, VSM could still be revealed by more sensitive measurements such as priming, discrimination threshold, or responding time.

CHAPTER 3. INDIVIDUAL DIFFERENCES IN VSM LIFETIME

This chapter will apply the new procedure described in section 2.1 to characterize partial-report performance for individual subjects and apply the model developed in section 2.2 to isolate VSM and VWM from the performance. The main concern of this chapter was the different VSM lifetimes exhibited by different subjects. Two additional experiments were conducted to assess some issues in the measurement of partial-report performance for revealing the VSM component.

3.1 Experiment 1: VSM Lifetime in Individual Subjects

With few exceptions (e.g. Appelman, 1980; Sperling, 1960), most studies of partial-report performance report data averaged across subjects. Long (1985) acknowledged extensive individual differences and suggested that such differences reduce the power of the procedures that are based on averaged data to detect a change in the performance. However, the individual differences in partial-report performance and the underlying VSM and VWM have not been specifically examined. The lack of such information is reflected by a recent chapter on individual differences in memory (Bors & MacLeod, 1996), which contained only individual differences in working memory and long-term memory, but not the differences in VSM.

3.1.1 Method

Subjects. Ten adults (four female, six male) ranged in age from 18 - 56 years (mean 30 years old) volunteered as subjects. One of them was the author. All had normal or corrected-to-normal vision. Subjects SL, SS, YS, KB, SH, and HG were naïve

to the task, and subjects WY, JH, LX, and JM had intensively practiced (about 10,000 trials within one month) in the standard method using different grating contrasts, mean grating luminances, spatial frequencies, or presentation durations.

Procedure. Each subject took a session of the standard test (see section 2.1).

3.1.2 Results & Discussion

The practiced subjects passed the assessment session in 20-40 trials. Naïve subjects passed the assessment criterion (80% correct in consecutive 20 trials) within 100 to 200 trials. Two naïve subjects, SS and SL could not pass the assessment even after extensive practice (>500 trials), so they were excluded from this experiment.

The probability of a correct response $P(t)$ at test delay t was calculated and plotted against test delay for each subject, as presented in Figure 3.1. Test delay was defined as the time interval from the offset of the display to the onset of the probe bar. The standard error σ_p for each probability value $P(t)$ was obtained by:

$$\sigma_p = \sqrt{\frac{P(t)[1-P(t)]}{n}} \qquad [3.1]$$

where $P(t)$ is the probability of a correct response at test delay t, n is the number of trials used to estimate the probability.

For each subject, an initial rapid decay followed by a short period of stable, above chance level performance was clearly shown. These are the features of a typical partial-report performance when the partial-report superiority is obtained.

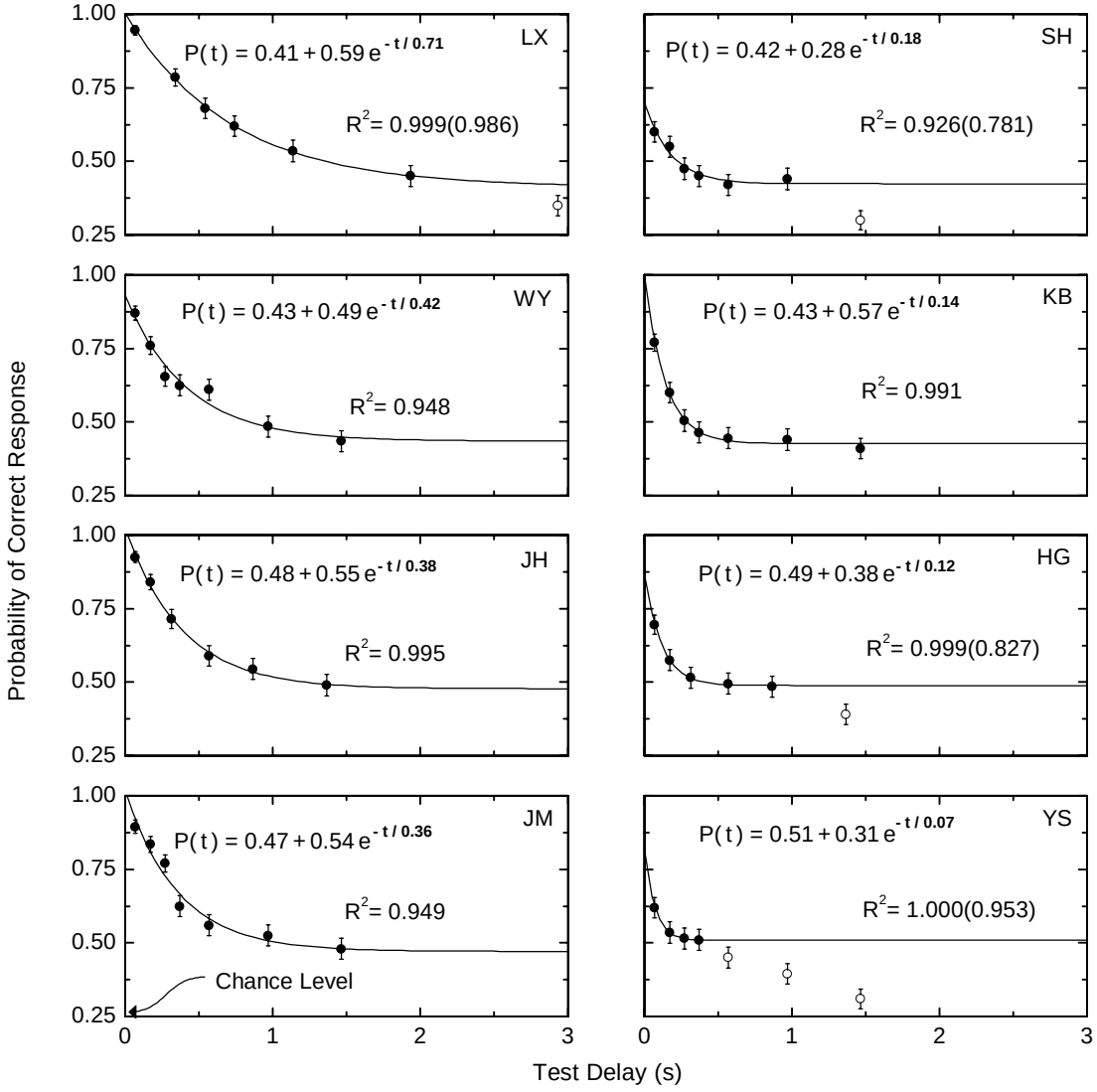

Figure 3.1. Partial-Report Performance for each of eight subjects. The left column contains plots for the practiced subjects, and the right column the naïve subjects. Error bars represent the standard errors (n = 192) of the probabilities. The solid lines represent the best exponential fitting functions in the form: $P(t) = A + B\,e^{-t/\tau}$. The open circles show collapse of the asymptote the initial decay and were not included in the fits. R^2 represents goodness of the fit. Values in the parenthesis for the R^2 are the values when the open circles were included in the fitting.

However, for subjects LX, SH, HG, and YS, the asymptote of the initial decay was not maintained for all the test delays. It dropped to chance or near chance level. This collapse of the asymptote indicates the failure of maintaining information in the VWM with full capacity. Because this study primarily concerned with the VSM lifetime and the requirements for applying the model (section 2.1) were satisfied by the clear initial decay and evident asymptote in the individual performance, the model was applied to the initial decay and its asymptote while the points fall bellow the asymptote in some subjects were not included in fitting the function [2.1]. The obtained best-fitting function was plotted for each subject in Figure 3.1.

The quality of the fit was assessed by R^2, the proportion of variance accounted for by the fit, adjusted for the number of free parameters:

$$R^2 = 1 - \frac{\sum_{i=1}^{n} (y_i - y_i')^2 \Big/ (n-k)}{\sum_{i=1}^{n} (y_i - \bar{y})^2 \Big/ (n-1)} \qquad [3.2]$$

Where y_i are the observed data values, y_i' are the predicted values, $\bar{y}$ is the mean of y_i, n is the number of data points, and k is the number of free parameters (Reed, 1976).

Please note that the asymptote of the best fitting function indicated the level of the performance maintained by the full capacity VWM, not the actual time course of VWM. To characterize the decay of the VWM, longer test delays should have been included. To apply the present model to isolate VSM and VWM and take the decay of VWM into consideration, the assumption of a prolonged constant VWM should be changed to account for its decay after a relatively short period.

3.1.3 Loss of Information from VWM

How can the collapse of the asymptote of the initial decay in partial-report performance be attributed to the loss of information from VWM? Equation [2.2] presents the relation between partial-report performance and its underlying memories without any assumption regarding the form of the VSM and VWM.

$$P'(t) = P_w(t) + P_i(t) - P_w(t)P_i(t)$$

$$= P_w(t) + P_i(t)[1 - P_w(t)]$$

Because the typical time course of VSM is about 0.25 s and it is conceivable that 0.5 s after the offset of the display, the VSM has decayed completely or nearly to a zero level. In the above equation, when $P_i(t) \rightarrow 0$, $P'(t) \rightarrow P_w(t)$. So any change in partial-report performance beyond 0.5 s should be solely attributed to the VWM.

As indicated in the left panel of Figure 3.1, the asymptotic performance was maintained at a stable above-chance level up to 1.5 s for the four practiced subjects. By contrast, the performance decreases to a near chance level near the delay of 1.5 s for three of four naïve subjects. These results indicate that full capacity VWM information could be kept longer in practiced subjects than in naïve subjects. For the practiced subject, the asymptotic performance would collapse to chance level if the test delay were long enough. This is indicated by the dropping of the last point below the asymptote at test delay of 2.9 s for LX. In a pilot study for WY when the test delays were further increased, the asymptote of the initial decay was maintained up to 2.5 s and then decays to nearly chance level appeared with longer delays.

Such collapse of the asymptote of the initial rapid decay in partial-report performance has not been recognized in the previous partial-report studies. One possible reason for this is that the decay of VWM starts at different test delay for different subjects as indicated in Figure 3.1. This made it difficult to detect a two-stage decay in averaged data. Another possibility is that that the intertrial intervals in the previous partial-report studies were much longer than the interval of 2 s in present experiment. For example, Keele & Chase (1967) used intertrial interval of 10 s and their subjects were able to maintain 2 to 4 items out of 10 items in the display for up to 5 seconds.

The collapse of the asymptote performance in partial-report task more likely occurs for naïve subjects or when intertrial interval is short. Although the asymptote performance was maintained up to 1.5 sec for the practiced subjects shown in the left panel of Figure 3.1, it was observed in the pilot studies that the asymptote collapsed at short test delays about 1 s when these practiced subjects were distracted by fatigue or hunger etc. Because the asymptote performance is solely supported by the VWM, the conditions for the collapse of the asymptote performance reveal the condition where VWM fail to maintain in full capacity.

The observation of the initial decay to an above chance asymptote followed by a further decay to chance level in partial-report performance shows cascade decaying pattern in a single memory task. Such cascade decay clearly indicates two memory components of different time course are involved in the partial-report task. Thus, when

the measurement of partial-report performance is accurate enough, the VSM and VWM could be dissociated by their temporal properties.

3.1.4 Inter-Subject Variance in Partial-Report Performance

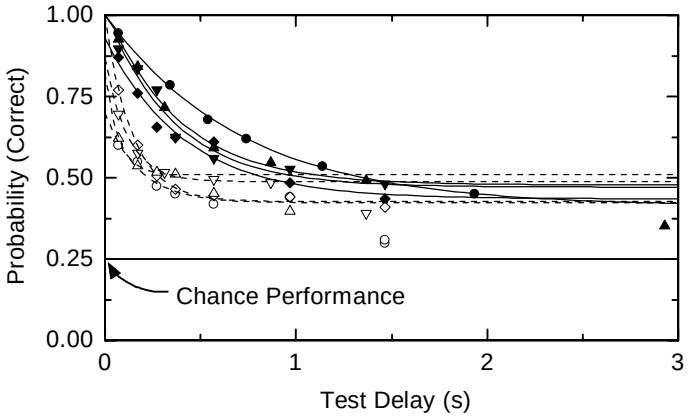

Figure 3.2. Comparison of partial-report performances in practiced and naïve subjects. The solid and dashed lines represent the best-fit exponential functions when the decay of the VWM was ignored, for practiced and naïve subjects respectively. Each type of symbol represents a different subject.

Figure 3.2 shows partial-report performance for each subject in a single plot to illustrate the inter-subject variance. For clarity, the error bars were not included in this figure. The functions clearly clustered into two groups depend on whether the subject was practiced. The main difference between the performance of the practiced subjects and that of the naïve subjects were that 1) the initial decay of the naïve subjects were more rapid than those of the naïve subjects indicating a shorter VSM lifetime for the naïve subjects, 2) the performance of the naïve subjects collapsed to chance level earlier than those of the practiced subjects.

3.1.5 VSM and VWM underlying the Performance

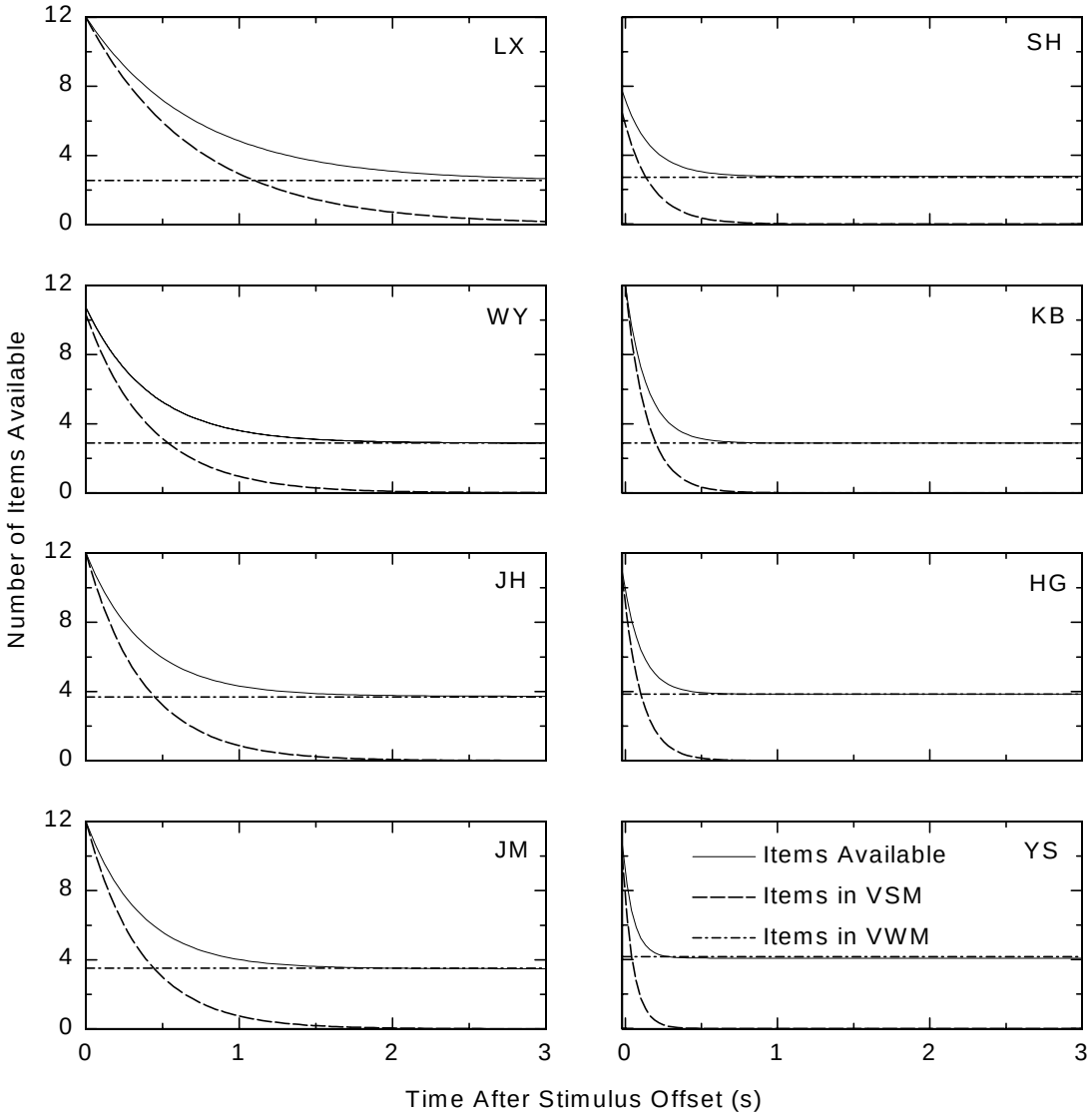

Figure 3.3. Partial-report performance, the deduced visual sensory memory (VSM) and visual working memory (C_w) for each subject.

Figure 3.3 presents the total visual information available at various times after the display offset and the underlying VWM and VWM deduced by the model presented in equations [2.11] and [2.12]. Because the parameters *A, B* and τ were obtained by fitting

only the initial decay and its asymptote with the assumption of a constant VWM, the VWM illustrated in this figure represents the level of the fully maintained VWM, not the time course of the VWM.

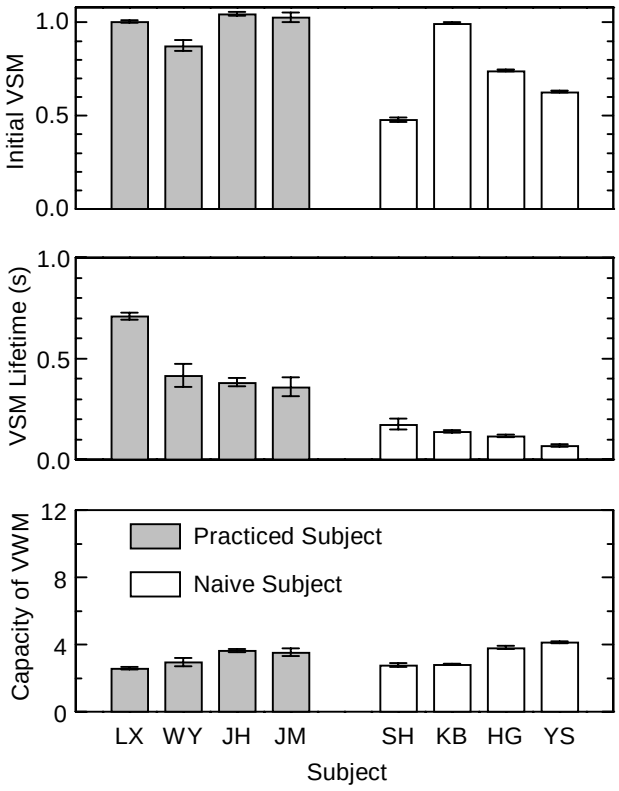

Figure 3.4. Initial level of visual sensory memory (P_i), lifetime of visual sensory memory (τ), and capacity of visual working memory (C_w) for each subject. Error bars represent the standard error of the values.

As discussed in section 2.2.2, function [2.3] and [2.4] with three parameters P_w, P_i, and τ completely describe the VSM and VWM which jointly support partial-report performance. To compare the memories underlying the performance across subjects,

Figure 3.4 presents these three parameters for each subject. Note that P_w was converted to C_w by equation [2.12] because it actually represents the capacity of the VWM.

Inter-subject difference in initial VSM level (P_i). The parameter P_i is the probability of a correct response based on VSM (or iconic memory) when probed right after the display offset with no delay. It represents the initial level of the VSM characterized. As indicated by the top panel of Figure 3.4, it was about the same for the practiced subjects but was more variable among the naïve subjects. Because the overall performance of the naïve subjects was poorer than that of the practiced subjects, it was expected that the initial VSM levels of the naïve subjects would be lower than those of the practiced subjects. The difference was found to be significant [(t (6) = -2.41, p < 0.05, one-tailed test]. Such an effect was also indicated in individual data presented in Fig. 3.5 where the performance at the shortest positive SOA was consistently enhanced in the second test for every single naïve subject.

Inter-subjects difference in VSM lifetime (τ). The difference between the lifetimes of VSM (τ) in the two groups was significant [t (6) = - 4.02, p < 0.05]. This suggests that practicing on this task enhance the VSM lifetime. This enhancement will be further illustrated in Experiment 3 & 6 using a within subject design.

The naïve subjects exhibited lifetimes shorter than those of the practiced subjects and their initial VSM level was lower than those of the practiced subjects. Further research is needed to elucidate the mechanisms of the enhancement of lifetime and the improvement of the initial VSM level. Yet shorter lifetime of the naïve subjects should

not be attributed to the lower initial VSM level. As will be shown in section 3.3.4, the VSM decay strictly follows an exponential function. For an exponential function, its lifetime is independent of the initial amplitude.

Inter-subject difference in capacity of VWM (C_w). There was a relatively small variance in C_w within each of these two groups, and the difference between the naïve and practiced subjects was not significant [t (6) = 0.48, p =0.65 > 0.05]. The mean of C_w of all the subjects was 3.3 ± 0.5 items in this experiment when items were presented at peripheral level of 6.5º. This result was consistent with the estimation for the VWM capacity of 4 items in the fovea and 2 in the peripheral (Wolford and Hollingsworth 1974). This capacity was found to be the number of integrated objects rather than the number of individual features (Luck & Vogel, 1997).

The capacity of the durable memory in Sperling's (1960) experiment was 4.5 items. Sperling (1960, p.4) noted that the correction for guessing would be about 0.4 letters for the 4/4/4 (12 letter) display. Thus the corrected value should be about 4 items in this experiment. This value was slightly higher than what would be expected from the estimation of Wolford and Hollingsworth (1974) because not all the items were presented in the fovea in Sperling's experiment. One possible reason for this slightly larger capacity might be a perceptual grouping between the items in rows and columns.

Such limited capacity of VWM has also been revealed in a task requiring subjects to track several identical moving spots. These experiments found that subjects can

accurately track 4 or 5 targets for a short period (Fisher, 1984; Kahneman, Treisman, & Gibbs, 1992; Pylyshyn & Storm, 1988; Yantis, 1992).

VWM, involving both item and spatial location information was found to involve cortical areas such as the inferior temporal (IT), posterior, ventrolateral and dorsal prefrontal cortex in both humans and monkeys (Baddeley, 1998; Miller, Li, & Desimone, 1991; Ungerleider, Courtney, & Haxby, 1998). By contrast, the cortical site for VSM has not been investigated. Chapter 6 of this study will explore the cortical location for the VSM.

The capacity of VWM was negatively correlated to VSM lifetime in both groups but the correlation was not significant in the combined groups. Such a trend in the data suggests that subjects having a shorter VSM lifetime find the task more difficult, and they concentrate more on the task with the result of a slightly higher VWM performance.

3.2 Experiment 2: Time Course of Retrieval and Partial-Report Performance

Well-practiced subjects in Experiment 1 passed the assessment right away, with occasional errors. The naïve subjects needed one to two hundreds of trials to reach the criterion of 80% correct in 20 consecutive trials. Even after the assessment was passed, performance in the no delay trials was not as good as that of the practiced subjects. This indicates that that the practiced subject has higher initial VSM level than the naïve subject. One explanation is that the practiced subjects can perceive the displays better than the naïve subjects. An alternative explanation is that the naïve subjects perceive the display as well as the practiced subjects, but it takes little longer for the naïve subjects to

retrieve to the indicated location, so that the VSM has experienced a slight decay when the VSM being retrieved. The failure of subjects SS and SL in the assessment of Experiment 1 might also be due to a slow retrieval because they both claimed that they could clearly see the patterns. Experiment 2 was designed to measure the time course of retrieval for these subjects.

3.2.1 Method

Subjects. Subject SS who failed the assessment in Experiment 1 participated in this experiment. Subject SL was not available for this experiment. Four naïve subjects (three male, one female) within the age range 18 - 28 years were recruited by payment. All had normal or corrected-to-normal vision.

Procedure. The standard test procedure described in section 2.1 was modified for this experiment. The change for the test session was that some test delays are negative which indicates the probe was presented before the display. The change for the assessment session was that the probe bar was presented 0.5 s before the display. Subjects RS, JS, and TD took the test for two sessions, whereas PC took additional two sessions to see whether his performance could be further improved. Test sessions were separated by one to two weeks.

3.2.2 Results and Discussion

Data for the four naïve subjects are presented in Figure 3.5. The time interval between the probe and the stimulus display in a trial was measured by stimulus onset asynchrony (SOA).

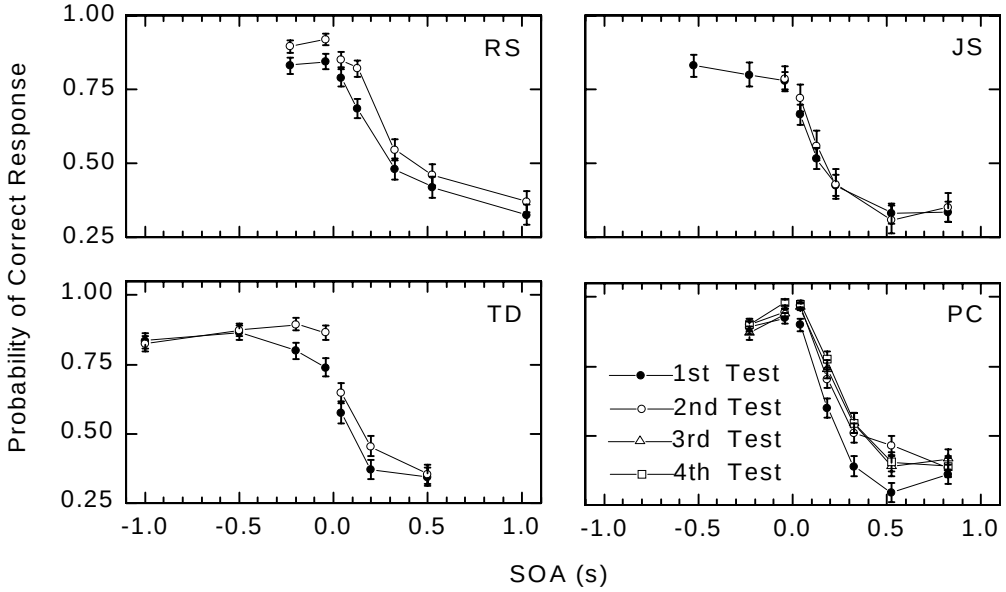

Figure 3.5. Probability of correct response as a function of the stimulus onset asynchrony (SOA) between the stimulus and the probe bar for naïve subjects. A negative SOA indicates that the probe bar was presented before the stimulus. The error bars represent the standard error (n = 192) of the probabilities.

The positive SOA side of the performance for each subject was similar to the performance of the naïve subjects presented in Figure 3.1. The response accuracy at the shortest positive SOA ranged from 57% to 97% in the first test session and increased for each subject in the second test session.

If the lower values of response accuracy at the shortest positive SOA were due to slower retrieval process, presenting the probe bar ahead of the display should increase the performance. This was the case for subjects JS and TD whose response accuracy at the shortest positive SOA was relatively low. Because the time course of the enhancement for the pre-cueing effect reveals the time course of retrieval for these subjects, these

results indicate that the lower accuracy in the condition of the simultaneous presentation of the display and probe bar is due to a slow retrieval process. The speed of retrieval could be enhanced in the first one to two thousand trials as indicated by the data of TD.

For PC and RS, whose response accuracy at the shortest positive SOA was relatively higher than other two subjects, presenting the bar probe right before the display slightly improves the performance, but presenting the probe bar earlier slightly decreases the response accuracy. This shows that the retrieval is a dynamic process: once the retrieval process reaches a location where the information is not yet available, it cannot be fully maintained at that location.

In conclusion, the low accuracy at short test delay for naïve subjects is at least partly due to a slower retrieving process as indicated by the negative-SOA performance in the first test session for TD. Such slower retrieving process could be speeded up by a session of practice to be nearly instantaneous. Other retrieval factors such as a misjudgment of the probed location might also contributed to the lower initial performance in the present partial-report task because for TD and JS, presenting the bar 1 s and 0.5 s respectively did not improve their performance to a near perfect level.

3.2.1 Time Course of Retrieval for Subject SS

The results for subject SS who did not pass the assessment are shown in Figure 3.6. The open circles show the results of SS in this experiment where the standard stimuli were used. Positive-SOA performance was maintained at an above chance level, indicating that a few items were transferred into WVM. The capacity of VWM for SS

was not lower than other subjects in this experiment. The main difference between the positive-SOA performance of SS's and other naïve subjects was the initial performance at the short test delays. This was clearly due to a slow retrieval process which is shown by the large improvement of the performance with more negative SOAs. Because his performance at -0.5 s was very accurate, his poor performance in present task was not likely due to a difficulty in judging the probed location.

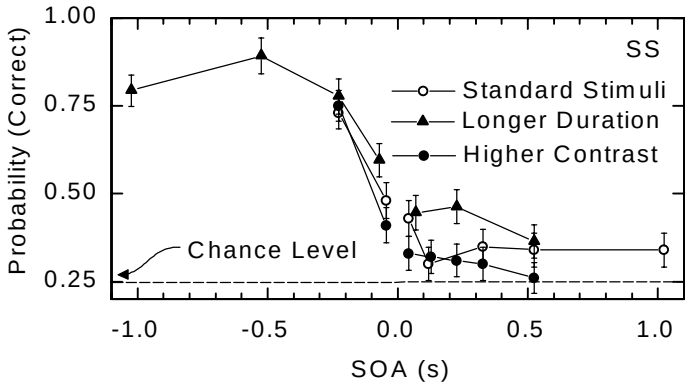

Figure 3.6. Partial-report performance for subject SS who failed the assessment in the standard visual sensory memory (VSM) test. A negative SOA indicates that the probe bar was presented before the stimulus. Different symbols represent different stimuli conditions. The error bars represent the standard error (n = 96) of the probabilities.

Subsequent tests with longer stimulus duration (200 ms) or higher contrast (90%) did not change the general pattern. In preliminary experiments these stimulus conditions enabled naïve subjects to pass the assessment in the standard test immediately. The improvement of performance with pre-cueing increased to a maximum at about SOA = -0.5 s and dropped slightly at SOA = -1 s. This pattern shows that the retrieval process for SS takes about 0.5 s and was not able to fully maintain at the indicated

location. The absence of VSM component in the performance is not due to lower contrast sensitivity or inability of the subject to see the display well, because the increase of the stimulus contrast did not improve the performance to a level comparable to other naïve subjects.

It could be conclude that the failure of SS in the assessment of the standard test is not due to deficits in visual perception, but a slower retrieval process. This is consistent with his claim that he can see the patterns clearly but "just cannot remember them". Such cases represent a small portion (about 5%) of the normal functioning people and are probably high risky in driving because they can not efficiently respond to transient visual scenes. Because a retrieval process involves the encoding of the orientation of the probe bar, shifting of covert attention to the indicated location, additional tests are needed to specify which of these processes underlying the performance is impaired.

3.3 Experiment 3: Effect of Practice on VSM Lifetime

In Experiment 1, the main difference between partial-report performance of the practiced subjects and that of the naïve subjects was that the VSM lifetime was longer for the practiced subjects. In addition, the initial VSM level in the practiced subjects is close to be perfect, while only one of four in the naïve group exhibits near perfect initial VSM. Such differences in VSM between the naïve and practiced subjects suggested that there is a practice effect on the VSM. Long (1980) noted such a practice effect in partial-report performance and suggested that it might account for the different results between experiments using naïve subjects and those using practiced subjects. However, no

experiment has been done to characterize the practice effect. Experiment 2 was to examine the practice effect using a within subject design.

3.3.1 Method

Subjects. Four of the subjects in Experiment 1 volunteered for this experiment. Two (YS, KB) were naïve and two (WY, LX) were practiced.

Procedure. After participating in Experiment 1, the four subjects took the standard partial-report test repeatedly 8 times for KB, 7 times for WY, and 5 times for LX and YS. The time interval between the test sessions ranged from 1 to 2 weeks. There was a 1 month inter-session interval between 4^{th} and 5^{th} sessions for KB, and between 3^{rd} and 4^{th} sessions for YS.

3.3.2 Results and Discussion

Results from the two naïve subjects and the two practiced subjects showed different patterns and are therefore reported separately.

Results of repeated tests for naïve subjects. The results of the repeated tests for the two naïve subjects are presented in Figure 3.7. The test in Experiment 1 was referred to as the 1st test session. Overall performance gradually improved with repeated tests for both subjects. An obvious difference between these two subjects were that the asymptote was always maintained up to 1.5 s for KB while not maintained beyond 0.56 s for YS in the first two test sessions. This indicates that YS was not able to maintain information in VWM with full capacity beyond 0.56 s in the first two test sessions. Relatively stable asymptotic performance was achieved after the second test session for YS.

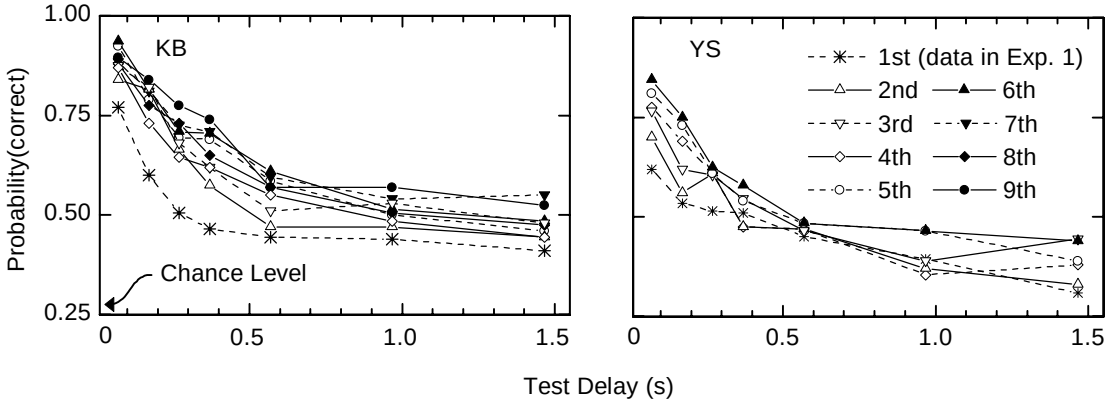

Figure 3.7. Partial-report performance in repeated tests for two naïve subjects. Different symbols represent different test sessions.

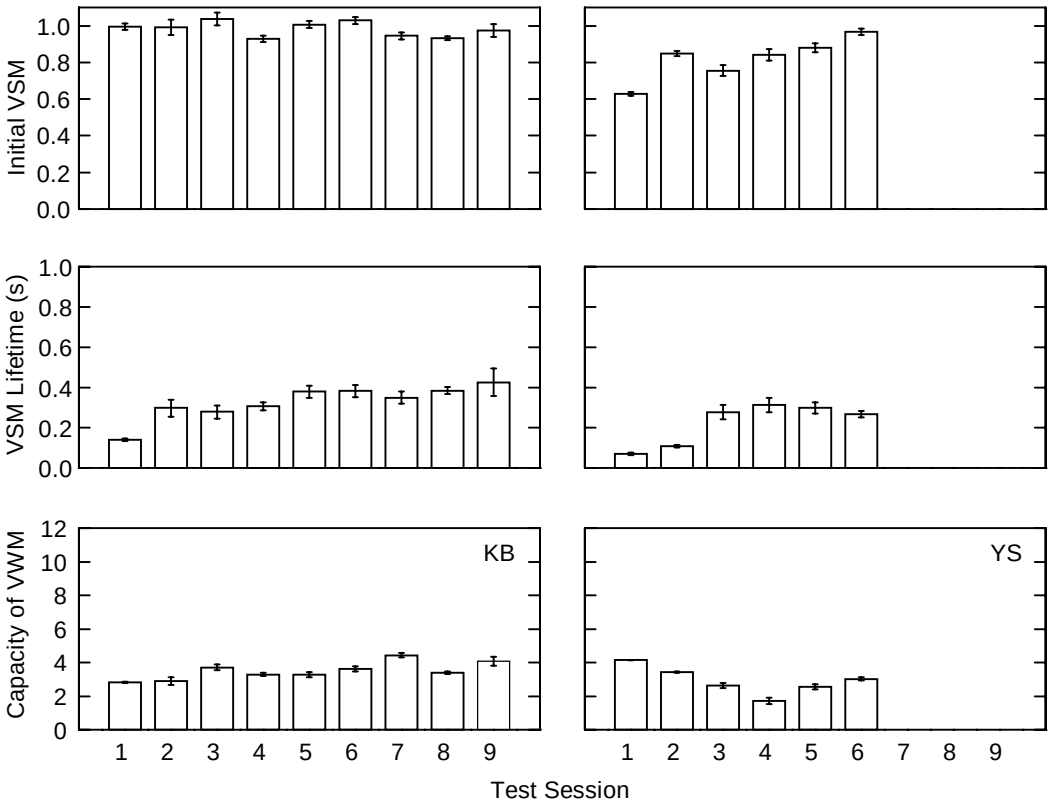

Figure 3.8. Initial level of visual sensory memory (P_I), lifetime of visual sensory memory (τ), and the capacity of visual working memory (C_w) in repeated tests for two naïve subjects. The error bars represent the standard error of the values.

Data of each test session were fit with the function in Equation [2.1]. VSM lifetime (τ) was obtained from the fits. The initial VSM (P_i), and capacity of VWM (C_w) were deduced by equation [2.10] and [2.12] respectively. Figure 3.8 presents the change of VSM and VWM in the repeated test sessions for these two subjects. The last two dots in the 1st and 2nd test sessions for YS, which were caused by the failure of maintain information in VWM with full capacity, were not included in the fitting.

The initial VSM level was continuously enhanced for YS. By contrast, for KB it was perfect in the first test. Moreover, the lifetime of VSM significantly increased from 1st to 2nd test for YS and from 4th to 5th test for KB. Repeating the test session would enhance the lifetime in the initial repetitions and reach a relatively stable level afterwards. There was no significant improvement of lifetime for YS in the last four test sessions, nor for KB in the last 5 test sessions. Although the lifetime of these two naïve subjects reached a stable level after 2 to 3 repeated tests, the results of Experiment 10 indicates that further massive repetition would continue to enhance the lifetime up to 20 session, but the enhancement was slow.

The capacity of VWM for KB was continuously enhanced, but the enhancement was slow and the total change was very small (less than one item). The capacity of VWM for YS showed an unusual "U" shaped change. This was mainly caused by the lower value in the 4th session. The large standard error for this session suggests that the small value was caused by the deviation of the decay pattern from an exponential function due to a failure to maintain information in VWM with full capacity.

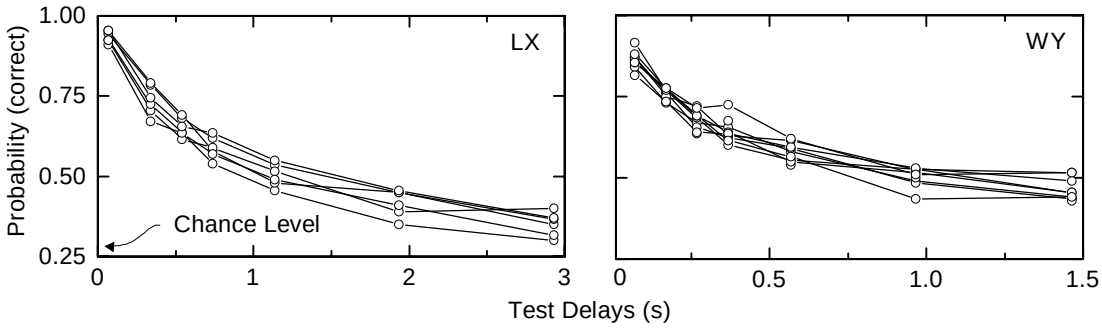

Figure 3.9. Partial-report performance in repeated tests for two practiced subjects. Note that the time scales in these two plots are different.

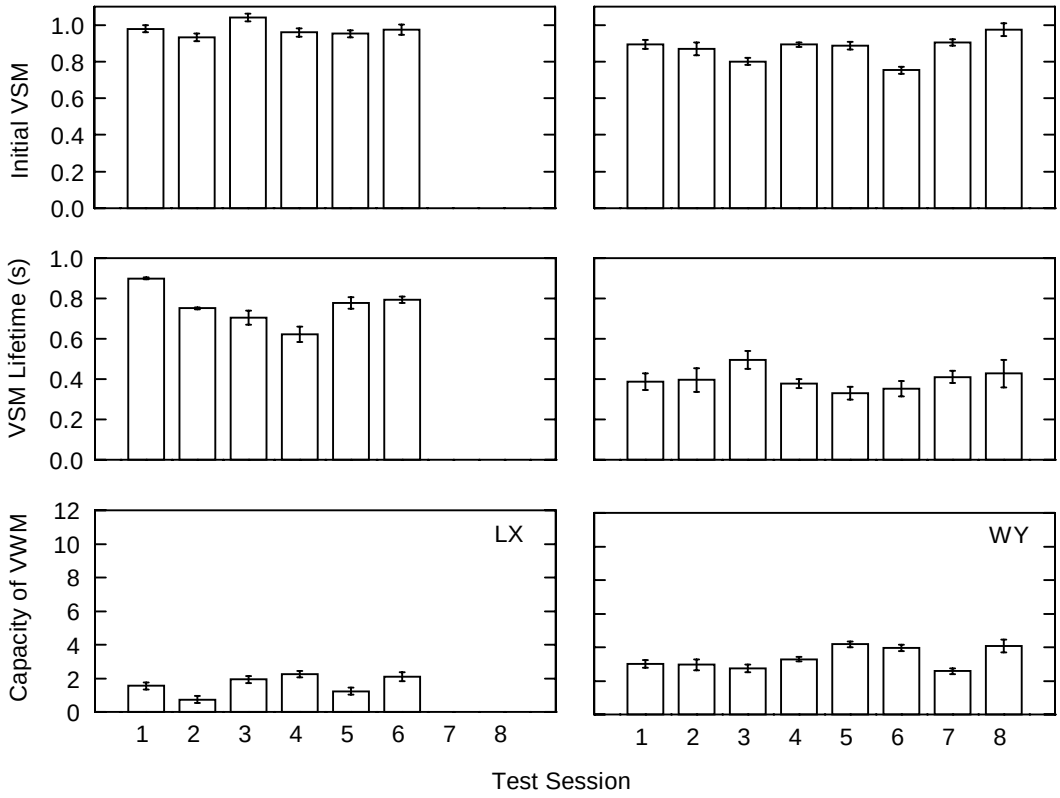

Figure 3.10. Initial level of visual sensory memory (P_I), lifetime of visual sensory memory (τ), and capacity of visual working memory (C_w) in repeated tests for two practiced subjects. The error bars represent the standard error of the values.

Results of repeated tests for practiced subjects. Figure 3.9 presents the results of the repeated tests for the two practiced subjects. The performances in the repeated tests for the two practiced subjects were much more stable than in the two naïve subjects.

Figure 3.10 shows the two memory components underlying performances in the repeated tests. There was no consistent significant across-sessions difference for practiced subjects in each aspect of VSM. The VSM lifetime of all the practiced subjects in Experiment 1 were about 0.2 s in the pilot studies when they just started participating this project. This suggests that their lifetime had been improved by the intensive practice. The stable performance of the two practices subjects in this experiment indicates their performance have reached the ceiling.

3.3.3 Practice Effect on VSM Lifetime: A New Dimension of Perceptual Learning?

The VSM has been considered as a passive sensory buffer and its activation is stimulus driven and should not be changed by experience. The observations of the enhancement VSM lifetime in this study indicates that the time course of the VSM could be enhanced by practice. It is not clear at this moment whether the enhancement of the lifetime is due to the repeatedly stimulation of the visual sensory system or due to the fact that the present task requires a longer lifetime to achieve better performance. The latter would predict that VSM lifetime could be reduced by practicing a task where subject has to suppress visual persistence to achieve better temporal resolution. The above two possibilities suggest different neural mechanisms underlying the lifetime change. An enhancement of VSM lifetime by repeated stimulation implies a change in synaptic

efficiency or other intrinsic properties of neurons in the early sensory area merely because of their repeated activation. The change of lifetime by task requirement implies a top-down modulation of the early visual sensory activity by higher cortical areas. There is evidence for a modulation of V1 activation by processing at the higher levels (e.g. Ishai & Sagi, 1995; Kosslyn et al., 1995; Le Bihan et. al., 1993).

The enhancement of VSM lifetime with practice is consistent with the dramatic enhancement of performance in other visual tasks by extended practice which is often regarded as perceptual learning (e.g. Cavanagh, 1993; Sagi & Tanne, 1994). The enhancement of lifetime reveals a new perceptual learning phenomenon and a new dimension by which the visual sensory system could be changed with practice.

Perceptual learning has been generally characterized as specifically related to stimulus parameters and retinal location, and shows no interocular transfer. This suggests that visual perceptual learning involves plastic changes at very early levels in the visual system, such as V1 where some units are monocularly driven. It could also be specific to the attended sensory feature (Ahissar & Hochstein, 1993) which suggests that learning could not be solely attributed to the changes of the processing in the sensory system. The practice effects can be acquired within a single experimental session and/or progressively from one session to the next one, often continuing to improve until thousands of trials have been performed. The effect could be maintained for 2-3 years (e.g. Karni & Sagi, 1993).

The enhancement of VSM lifetime with practice shares some features of perceptual learning revealed in other paradigms. The lifetime is rapidly increased in the first one to two thousand trials and increased slowly with additional practice. The improved performance was maintained for at least 3 and 8 months respectively for JM and LX. It is not clear whether the enhanced lifetime is specific to the retinal location of 6.5° or the attended stimulus feature of orientation. Identification of these specificities will shed light on the mechanism of the lifetime enhancement.

3.3.6 Form of VSM Decay

The mathematical form of the memory decay function has been a question of concern for the theorists because "An important step in the evolution of science, including the behavioral science, is the identification of lawful empirical regularities" (Anderson & Tweney, 1997, p. 409). The decay of VSM has been widely assumed to be exponential (e.g. Di Lollo & Dixon, 1988; Massaro & Loftus, 1997; Sperling, 1970), but no effort was made to test this assumption. The exponential decay of auditory sensory memory has been revealed psychophysically with the central-tendency paradigm (Lu et al., 1992). In this section, the exact mathematical form of the VSM decay was examined by assessing the fitness of the exponential function [2.1] to the data with very low standard error obtained by averaging the stable performance from the repeated VSM tests in this experiment (all the test sessions for the two practiced subjects, sessions 3-6 for subject YS, and sessions 5-9 for KB). These results and the corresponding best-fit exponential decays are presented in Figure 3.11.

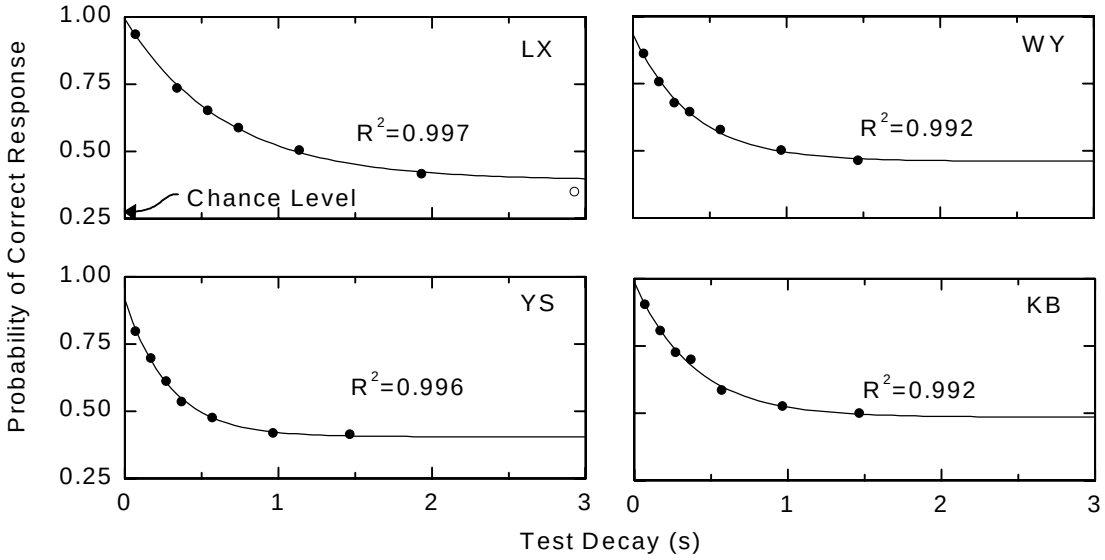

Figure 3.11. Form of visual sensory memory decay. The standard errors for the probabilities are smaller than the symbol size. The solid lines represents the best-fit exponential function in the form: $P(t) = A + B\,e^{-t/\tau}$. R^2 represents the goodness of fit. The open circle is not included in the fit (See 3.1.2. for relevant discussion).

The quality of the fit was assessed by R^2 calculated by [3.2]. The function $P(t) = A + B\,e^{-t/\tau}$ accounts for over 99% of the variance for the data of each subject. Such a near-perfect fitting indicates that the initial rapid decay in partial-report performance caused by the decay of VSM is strictly exponential.

3.4 Conclusions

1). Application of the procedure and model developed in Chapter 2 revealed the exponential decay of VSM and characterized its lifetime for each subject. The lifetimes for the eight subjects range from 0.07 to 0.7 s, and majority of the inter-subject differences were due to intensive practice with the present task.

2). A few subjects (~5%) did not exhibit the VSM component in the performance due to a slower retrieving process. For most naïve subjects, the time course of retrieval does not cause a problem for revealing the VSM component in their performance.

3). With repeated tests for naïve subjects, VSM lifetime exhibits a substantial increase in the first 2000 to 3000 trials and followed by a slower enhancement and finally reaches a ceiling of about 0.4 s (except LX, who reached 0.7 s). Such enhancement of VSM lifetime reveals a new dimension by which perceptual learning might occur.

CHAPTER 4. EFFECT OF STIMULUS PARAMETERS ON THE LIFETIME OF VSM

VSM has been described as a stimulus-driven passive storage of visual information. However, it is not clear how its lifetime is influenced by the stimulus parameters is not clear in the previous studies. This part of the study examines which features of stimulus influence the VSM lifetime. This was accomplished by changing the parameters of the standard stimulus (Fig. 2.1). Such information is also needed to identify the neural substrate of VSM. To identify a neural activity as the substrate of VSM, it is critical to show that its lifetime is sensitive to the same stimulus parameters as VSM.

The stimulus parameters chosen in this study were the duration and intensity of the stimulus because there has no current agreement regarding how these parameters affect the time course of VSM, characterizing how these parameters affect the time course also gives us a basis for determining if similar effects are present in physiological measures. In addition, such information will shed light on theoretical issues regarding the relationship between VSM and visible persistence. Coltheart (1980) argued that VSM is not visible persistence, because partial-report performance, which defines VSM, is not affected by the stimulus duration and stimulus intensity, while visible persistence is inversely affected by both parameters.

Previous studies assessing these effects were primarily based on the examination of the change of overall performance, which does not necessarily indicate the change of

the VSM lifetime. Furthermore, it was pointed out that the absence of these effects was probably due to the lack of the sensitivity of the procedures (Long, 1984). The experiments of this chapter exploited the standard procedure and the model developed in Chapter 2 to assess the influences of these stimulus parameters on the VSM lifetime specifically.

Experiment 4 examined the effect of stimulus duration on the VSM lifetime, while experiments 5 through 9 examined the stimulus intensity effects on VSM lifetime in detail. Previous studies of the stimulus intensity effect involved changing the luminance of stimuli (letters and digits) relative to that of the background. Such a manipulation changes both the contrast of the contours and the overall luminance of the display. In this study with sinusoidal gratings, it was possible to present gratings with a mean luminance that is the same as the background, so that it is possible to change the contrast without changing the overall luminance. In addition, the stimulus conditions were carefully chosen to avoid the production of a retinal afterimage, so that the partial-report superiority could be attributed to VSM.

4.1 Experiment 4: Effect of Stimulus Duration on VSM Lifetime

The influence of stimulus duration on the time course of VSM has been assessed by examining its effect on partial-report performance, but the results have been inconsistent. For example, partial-report performance was not affected by stimulus duration in Sperling (1960), Di Lollo (1978), and Yeomans & Irwin (1985), but an inverse effect was found by Di Lollo and Dixon (1988, 1992), as well as by Dixon and Di

Lollo (1991). What accounts for these differences is not clear. Nevertheless, the effect of stimulus duration on VSM lifetime has not been specifically assessed in these studies. This experiment was to examine the effect of stimulus duration in VSM lifetime.

4.1.1 Method

Subjects. Three subjects (one was the author) having intensive experience (10,000 trials within a month) with the present task volunteered as subjects. All had normal or corrected-to-normal vision.

Procedure. A session of trials of the standard test (section 2.1) were randomly mixed with a second set of trials. The trials of the second set were the same as that of the standard test except that the stimulus duration was increased to 200 ms. These two session of trials were completed in two consecutive days.

4.1.2 Results and Conclusions

Partial-report performance for the two stimulus conditions for each subject are presented in Figure 4.1. The performances under these two conditions was not significantly different for LX [$t(6) = 1.24$, $p > 0.10$] and WY [$t(6) = -2.21$, $0.01 > p > 0.05$], but was significant for JM [$t(6) = 3.51$, $p < 0.05$], with the performance being more accurate for stimuli of short duration, especially at the short test delays. The results for JM showed an inverse stimulus duration effect on partial-report performance.

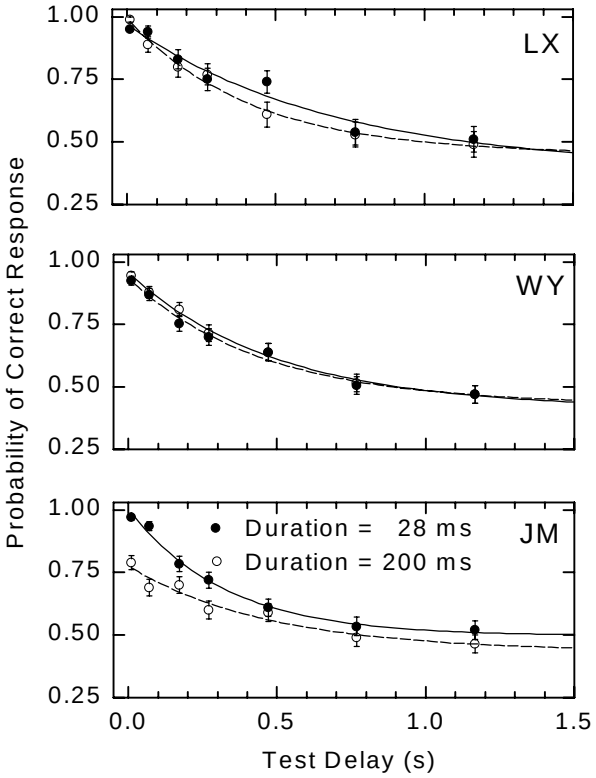

Figure 4.1. Effect of stimulus duration on partial-report performance for three subjects. The solid and dashed lines represent the best-fit exponential function for performance in the short and long stimulus duration respectively.

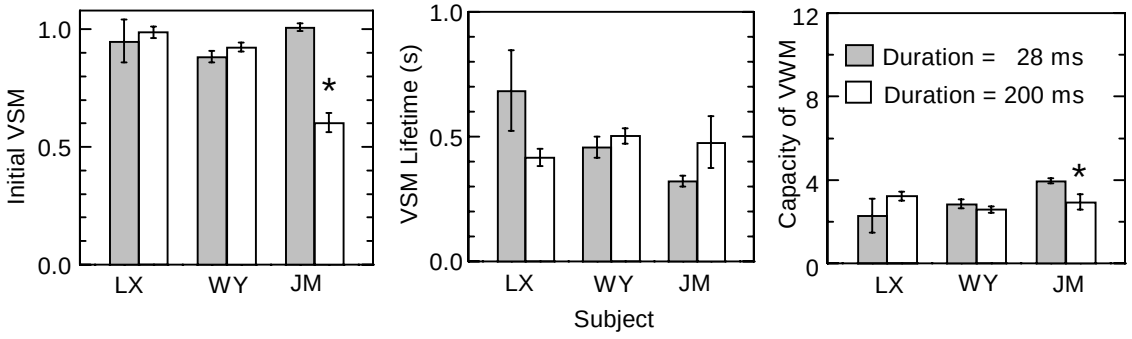

Figure 4.2. Effect of stimulus duration on initial level of visual sensory memory (P_i), lifetime of visual sensory memory (τ), and capacity of visual working memory (C_w). Error bars represent the standard error of the values.

The specific effects of stimulus duration on the VSM and VWM are presented by contrasting the parameters of these two memories for stimulus of different duration for each subjects in Figure 4.2. The parameters were deduced from the model introduced in section 2.1.

For subject LX and WY, there was no significant effect of stimulus duration on any of the three parameters. For JM, a significant inverse effect was found for the initial level of VSM ($z = 9.23$, $p < 0.05$) and capacity of VWM ($z = 2.63$, $p < 0.05$). The stimulus duration effect on the VSM lifetime of JM was not significant ($z = -1.50$, $0.01 > p > 0.05$).

In conclusion, increasing the stimulus duration from 28 ms to 200 ms had a significant effect on partial-report performance for one of three subjects. The effect for this subject was specific to a large reduction of initial VSM level and a small reduction for the capacity of VWM. What led to this individual difference is unknown. Such results call attention to individual differences in partial-report studies.

The inverse intensity effect on partial-report performance for JM is consistent with some reports of such effects presented in group data (Di Lollo & Dixon, 1988, 1992; Dixon and Di Lollo, 1991). Because individual data were not reported in the above-cited studies, it is not clear whether such an inverse duration effect on the overall performance was also specific to some subjects in these studies.

For subject JM of this experiment, a significant decrement of initial VSM level by increasing stimulus duration was accompanied by an increment of VSM lifetime.

Although the lifetime increment was not significant, the opposite direction of the changes indicates that it is not appropriate to assess the time course of VSM by examining the overall performance level.

4.2 Experiment 5: Effect of Stimulus Contrast on VSM Lifetime

This experiment examined the effect of changing the contrast of the sinusoidal gratings while maintaining the mean luminance of the stimuli remained the same as that of the background. In this case, the presentation of either the low and high contrast stimuli involves no change in overall luminance.

4.2.1 Method

Subjects. Four subjects with intensive experience in the present task volunteered for this experiment. All had normal or corrected-to-normal vision.

Procedure. A session of trials of the standard test (section 2.1) were randomly mixed with a second set of trials. The trials of the second set were the same as that of the standard test except that the contrast of the gratings was increased to 90% while the mean luminance of the gratings was maintained the same as the background. These two session of trials were completed in two consecutive days.

4.2.2 Results and Conclusions

Partial-report performance for stimuli of different contrast are presented in Figure 4.3 by plotting the probability of a correct response against the test delay.

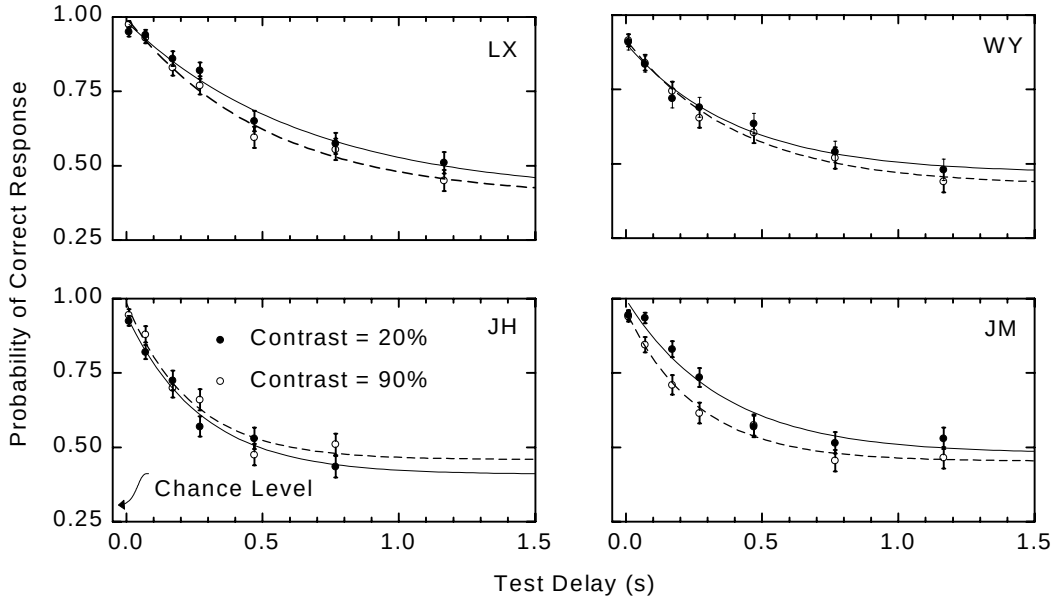

Figure 4.3. Effect of stimulus contrast on partial-report performance. Trials with stimuli of different contrast were mixed in a test session. The solid and dashed lines represent the best-fit function for contrasts of 20% and 90% respectively.

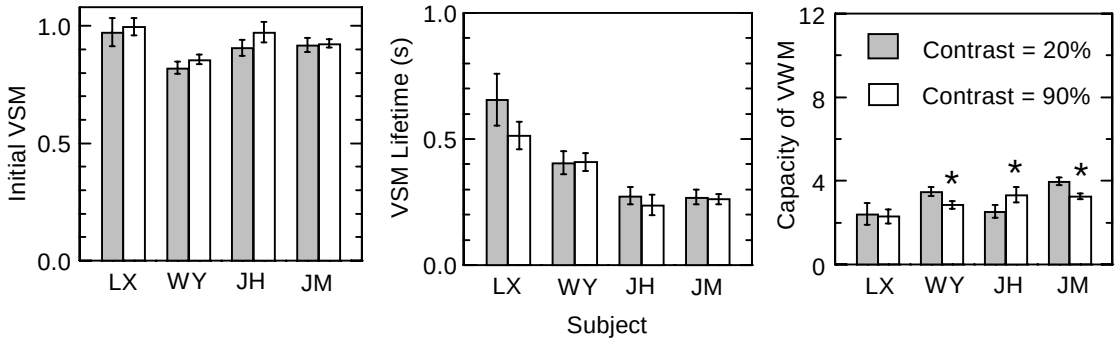

Figure 4.4. Effect of stimulus contrast on initial level of visual sensory memory (P_i), lifetime of visual sensory memory (τ), and capacity of visual working memory (C_w). Trials with stimuli of different contrast were mixed in a test session. Error bars represent the standard error of values.

The effect of stimulus contrast on partial-report performance was significant for LX [t (6) = 2.511, $p < 0.05$] and JM [t (6) = 3.417, $p < 0.05$], but not significant for WY [t (6) = 1.381, $p > 0.10$] and JH [t (5) = -0.635, $p > 0.10$].

The specific effects of stimulus contrast on VSM and VWM are presented by contrasting the parameters for these two memories in the two experimental conditions for each subject as shown in Figure 4.4. The parameters were deduced from the model introduced in section 2.1.

Contrast effect on initial VSM. Although there was a consistent slight enhancement of initial VSM level by increasing the stimulus contrast for all subjects, the effect was not significant for either the group data [t (3) = -2.54, $0.10 > p > 0.05$] or for each subject (z = -0.33, $p > 0.10$ for LX; z = -1.07, $p > 0.10$ for WY; z = -1.17, $p > 0.10$ for JH; and z = -0.14, $0.10 > p > 0.05$ for JM). The 20% stimuli were clearly visible for each subject in the assessment before the test, but subjects reported that the stimuli were invisible in a few trials. The 90% contrast stimuli were always clearly visible. Thus, the small enhancement of contrast is consistent with the enhancement of the visibility of the stimuli by increasing the contrast of the gratings.

Contrast effect on VSM lifetime. Although there was a consistent slight decrement of VSM lifetime by increasing the stimulus contrast for each subject, the effect was not significant for either the group data [t (3) = 1.38, $p > 0.10$] or for each subject (z = 1.23, $p > 0.10$ for LX; z = -0.05, $p > 0.10$ for WY; z = 0.68, $p > 0.10$ for JH;

and z = -0.2, $p > 0.10$ for JM). This indicates that increasing stimulus contrast slightly shortens the VSM lifetime, but the effect was too small to reach a significant level.

Contrast effect on the capacity of VWM. The effect of stimulus contrast on the capacity of VWM was not consistent across subjects. There was a significant decrement of C_W by enhancing contrast for WY ($z = 2.27$, $p < 0.05$) and JM ($z = 3.13$, $p < 0.05$), but there was a significant increment effect for JH ($z = -1.69$, $p < 0.05$). There was no significant effect for LX ($z = 0.18$, $p > 0.10$).

Therefore, increasing the stimulus contrast from 20% to 90% causes a small but significant enhancement in partial-report performance for two of four subjects. It also has a small decrement effect on VSM lifetime for each of four subjects, but the effect was too small to be significant. It also produces small but significant effects on VWM for three of four subjects, but the direction of the effect for these subjects was not consistent.

It should be noted that further decrease of the contrast resulted in a larger number of trials in which the display was not visible, and the data were much more variable. Thus, the contrast range used in this experiment covered the range that provides clear visibility and stable performance.

4.3 Experiment 6: Effect of Luminance Increase on VSM Lifetime

This experiment examined the effect of the overall luminance change in the stimuli on partial-report performance and the underlying memories. In this experiment, the performance for the equal-luminance stimuli which involve no change in overall

luminance upon presentation was compared with that for higher-luminance stimuli which involve a transient increment of the overall luminance upon stimulus presentation.

4.3.1 Method

Subjects. Four subjects with intensive experience with the present task volunteered as subjects for this experiment. All had normal or corrected-to-normal vision.

Procedure. A session of trials of the standard test (section 2.1) were randomly mixed with a second set of trials. The trials of the second set were the same as that of the standard test except that the mean luminance of the gratings was increased by 6.5 cd/m^2. Thus the mean luminance of the gratings was 6.5 cd/m^2 above that of the background. These two session of trials were completed in two consecutive days.

It should be noted that the contrast of the gratings was slightly changed by luminance increase; however, it was shown in Exp. 5 that such a contrast change had no significant effect on any aspect of the performance. Thus, these two stimulus conditions mainly differ whether the stimulus presentation involve an overall luminance change.

4.3.2 Results and Conclusions

Partial-report performances for the two stimulus conditions for each subject are presented in Figure 4.5 by plotting the probability of a correct response against test delay. The increment of the mean luminance of the gratings decreased the overall partial- report performance for each of four subjects ($z = 3.22$, $p < 0.05$ for LX; $z = 8.67$, $p < 0.05$ for WY; $z = 10.0$, $p < 0.05$ for JH; and $z = 3.22$, $p < 0.05$ for JM).

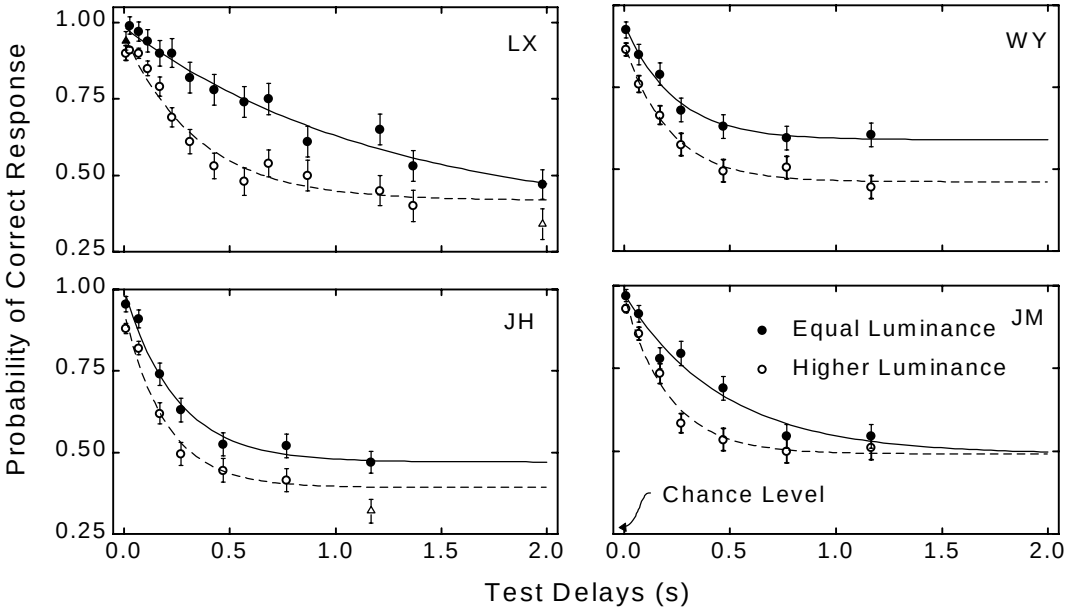

Figure 4.5. Effect of luminance increase on partial-report performance. Trials with stimuli of different luminance were mixed in a test session. The solid and dashed lines represent the best-fit exponential function for the performance of equal-luminance and higher-luminance stimuli respectively. Error bars represent the standard error of the probabilities.

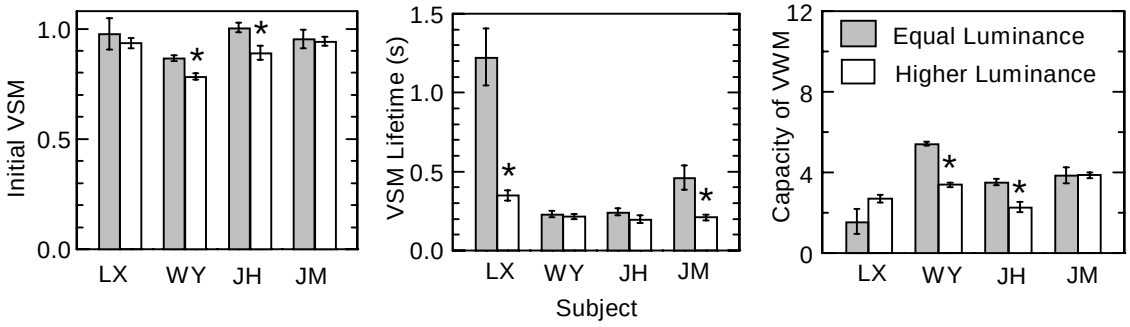

Figure 4.6. Effect of luminance increase on initial level of visual sensory memory (P_i), lifetime of visual sensory memory (τ), and capacity of visual working memory (C_w). Trials with stimuli of different luminance were mixed in a test session. Error bars represent the standard error of the values.

The specific effects of luminance increase on VSM and VWM are presented in Figure 4.6 by contrasting the parameters of these memories in the two conditions for each subject. The parameters were deduced from the model introduced in section 2.1.

Effect of a luminance increment on initial VSM. There was a consistent slight decrement of initial VSM level by increasing stimulus luminance for each subject. The effect was significant for WY ($z = 4.24$, $p < 0.05$) and JH ($z = 2.94$, $p < 0.05$), but not significant for LX ($z = 0.59$, $p > 0.10$) and JM ($z = 0.23$, $p > 0.10$). This indicates that an increment of stimulus luminance relative to the background slightly decreases the initial VSM level, although the effect was too small to be significant for each subjects.

Effect of a luminance increment on VSM lifetime. Although there was a consistent decrement effect on VSM lifetime by increasing the stimulus luminance above the background for each subject, the effect was large and significant for LX ($z = 4.77$, $p < 0.05$) and JM ($z = 3.18$, $p < 0.05$), not significant for WY ($z = 0.63$, $p > 0.10$) and JH($z = 1.41$, $0.10 > p > 0.05$). This indicates that increasing the stimulus luminance above the background shortens VSM lifetime for some subjects, but not for others in this experimental condition.

Effect of a luminance increment on the capacity of VWM. There was no consistent effect of luminance increment on the capacity of VWM for these subjects. There was a significant decrement of VWM capacity by enhancing luminance for WY ($z = 14.44$, $p < 0.05$) and JH ($z = 4.16$, $p < 0.05$), but a significant increment effect for

LX ($z = -1.72$, $p < 0.05$). There was no significant effect for JM ($z = -0.03$, $p > 0.10$). The effect on the group was not significant [$t(3) = 0.776$, $p > 0.10$].

In conclusion, the effect of a luminance increase on the two memories was not consistent for these four subjects: it reduces the initial VSM level and VWM and leaves VSM lifetime unaffected for two subjects (WY and JH), but decreases the VSM lifetime and leaves the initial VSM level and VWM unaffected for the other two subjects (LX and JM).

Particularly striking was that the luminance increment markedly reduced the VSM lifetime for two subjects (LX and JM), but not for the other two (WY and JH). The VSM lifetimes for the higher luminance stimuli for WY and JH are, however, significantly shorter than for the equal luminance stimuli tested in Experiment 1. This indicates that the absence of the inverse luminance effect for WY and JH in this experiment was due to the fact that the lifetimes for the equal luminance stimuli are shortened by being mixed with the higher luminance stimuli for subjects WY and JH.

4.4 Experiment 7: Effect of Luminance Increase on VSM Lifetime: Separate Tests

Experiment 7 was to measure the VSM lifetime for higher luminance stimuli when they were not mixed with the isoluminant stimuli. The results will be compared with the performance for equal-luminance stimuli tested separately in previous experiments to assess the effect of a luminance increase without interactions.

4.4.1 Method

Subjects. Three of the four subjects of Experiment 6 volunteered as subjects for this experiment. All had normal or corrected-to-normal vision.

Procedure. The procedure was the same as the standard test (section 2.1) except that the mean luminance of the gratings was increased by 6.5 cd/m^2. Thus the mean luminance of the gratings was 6.5 cd/m^2 above that of the background.

4.4.2 Results and Conclusions

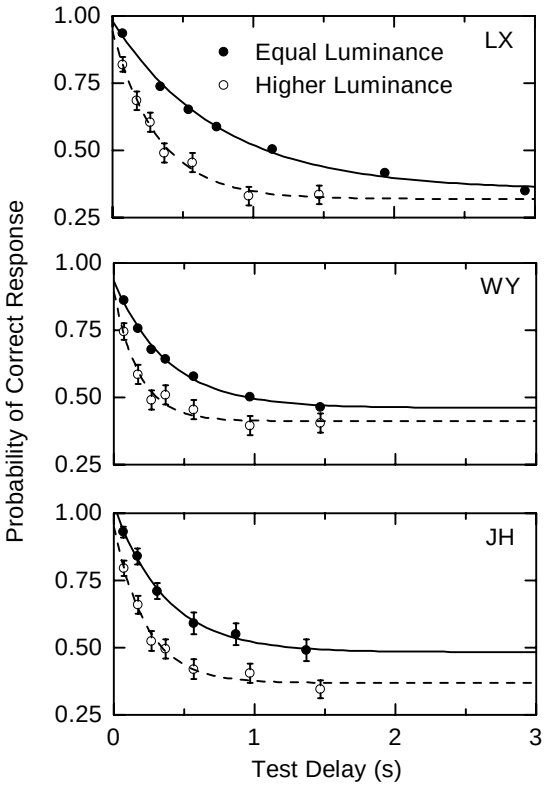

Figure 4.7. Effect of luminance increase on partial-report performance in separate tests. The solid and dashed lines represent the best-fit exponential function for the equal-luminance and higher-luminance stimuli respectively. Error bars represent the standard errors for the values. The standard error for the dots with no error bar is smaller than the symbol size.

Partial-report performances for the higher luminance stimuli when they were tested separately are presented in Figure 4.7. These performances were compared with the performances for the equal-luminance stimuli (Figure 2.1) in separate test sessions for each subject. The equal luminance data for LX and WY were from Figure 3.11 and from Figure 2.1 for JH.

The results were similar to those of Experiment 6: a significant effect of the luminance increase on performance was found for each subject. The specific effect on VSM and VWM were presented by contrasting the parameters of these memories in the two stimulus conditions for each subject as shown in Figure 4.8. The parameters were deduced from the model developed in section 2.1.

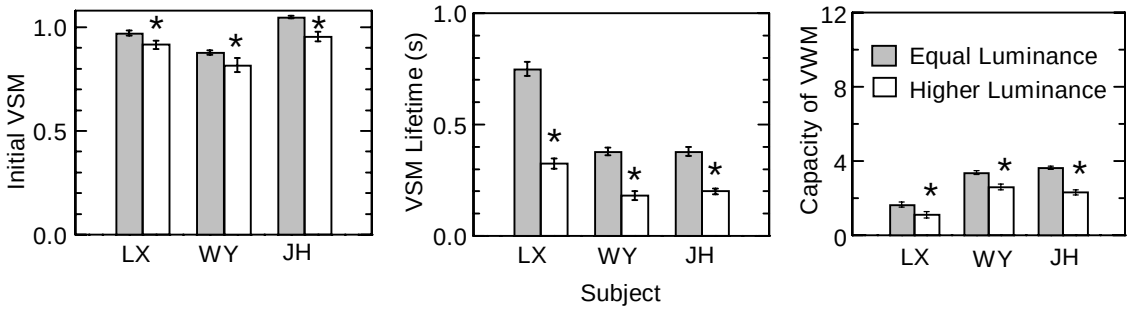

Figure 4.8. Effect of luminance increase on initial level of visual sensory memory (P_i), lifetime of visual sensory memory (τ), and capacity of visual working memory (C_w). Stimuli of different luminance were tested in separate test sessions. Error bars represent the standard error of the values.

When the equal-luminance and higher-luminance stimuli were separately tested in different sessions, there was a consistently significant decrement of initial VSM level with an enhanced stimulus luminance for LX ($z = 2.24$, $p < 0.05$), WY ($z = 1.90$, $p <$

0.05), and JH ($z = 4.47$, $p < 0.05$). Enhancing the stimuli luminance above the background significantly reduces VSM lifetime for LX ($z = 11.93$, $p < 0.05$), WY ($z = 7.01$, $p < 0.05$), and JH ($z = 8.05$, $p < 0.05$). Enhancing the stimulus luminance also significantly reduces VWM capacity for LX ($z = 2.48$, $p < 0.05$), WY ($z = 4.19$, $p < 0.05$), and JH ($z = 8.05$, $p < 0.05$).

In conclusion, when the two types of stimuli were used in separate test sessions, an increase in the mean luminance of the gratings significantly decreases initial VSM level, VSM lifetime, and VWM capacity for each of the three subjects.

4.4.3 Possible Mechanisms for the Effect of a Luminance Increase on VSM Lifetime

A slight increase of the mean luminance of the standard stimuli (Figure 2.1) above that of the background shortens the VSM lifetime for each of the three subjects in this experiment. As shown in Experiment 6, it also shortens the VSM lifetime for the standard equal-luminance stimuli if trials of these two types of stimuli were mixed in a test session. These results suggest that the presentation of the higher-luminance stimuli increases the adaptation level of the visual system and shortens the lifetime of the sensory memory system in general. This is called the *adaptation hypothesis*.

The adaptation hypothesis suggests that the VSM lifetime is determined by the adaptation level of the system. It is equally possible that the VSM lifetime is under the influence of the stimulus properties. Specifically, the luminance increase effect might be due to the shift of the spatial frequency channels in the visual pathway (Graham, 1981; Legge, 1978; Shapley & Lennie, 1995). When the mean luminance of the gratings was

increased, the power of the lower spatial frequency components in the stimuli was largely enhanced. Thus, the processing of information was shifted toward the low spatial frequency channels which are more transient in temporal dynamics, thus resulting in a shorter lifetime. This is called the *spatial-frequency channel hypothesis*.

Both mechanisms are consistent with the weak effect of a contrast change as observed in Experiment 5. According to the adaptation hypothesis, changing the contrast while maintaining the overall luminance the same as the background does not change the adaptation level of the system, thus the lifetime of the sensory system is not changed. The weak inverse contrast effect might be due to the possibility that the contrast change slightly changes the adaptation level due to the nonlinearity in the subjective scaling of luminance. According to the spatial-frequency channel hypothesis, changing the contrast of the sinusoidal gratings primarily enhances the power of the spatial frequency of those gratings which are the main components in the spatial frequency spectrum of the stimuli. Therefore, the peak of the spatial frequency spectrum is not shifted, thus the lifetime of the coherent activity of the channels involved remain unchanged. However, the low spatial frequency components defining the global spatial arrangement of the display is enhanced, which results in a slight increase in the power of the low spatial frequency components in the display and produces the small decrement of VSM lifetime.

However, these two hypotheses have opposite predictions for the change in VSM lifetime when the mean luminance of the standard stimuli is decreased below the background. The adaptation hypothesis predicts that a luminance decrease has an

opposite effect on the lifetime than a luminance increase because these manipulations drive the adaptation level in opposite directions. The spatial-frequency channel hypothesis predicts that the luminance decrease has the same effect on the lifetime as a luminance increase, because either an increase or decrease of the mean luminance of the isoluminant standard stimuli equally enhance the power of the very low spatial frequency components. The following experiment will test these hypotheses.

4.5 Experiment 8: Effect of Luminance Decrease on VSM Lifetime: Separate Test

This experiment further explored the mechanism for the effect of luminance change on the VSM lifetime. As discussed in Experiment 7, the *adaptation hypothesis* and the *spatial-frequency channel hypothesis* have different predictions for the effect of a luminance decrease on the lifetime of VSM. This experiment tested these hypotheses by examining the effect of a luminance decrease on the VSM lifetime.

4.5.1 Method

Subjects. Two of the three subjects in Experiment 7 volunteered as subjects for this experiment. All had normal or corrected-to-normal vision.

Procedure. The procedure was the same as the standard test (section 2.1) except that the mean luminance of the gratings was decreased by 6.5 cd/m^2. Thus the mean luminance of the gratings was 6.5 cd/m^2 below that of the background.

4.5.2 Results and Conclusions

Partial-report performance for stimuli of lower luminance are presented in Figure 4.9. Also presented in the figures are the data for the equal-luminance stimuli presented in Figure 3.11 for these two subjects.

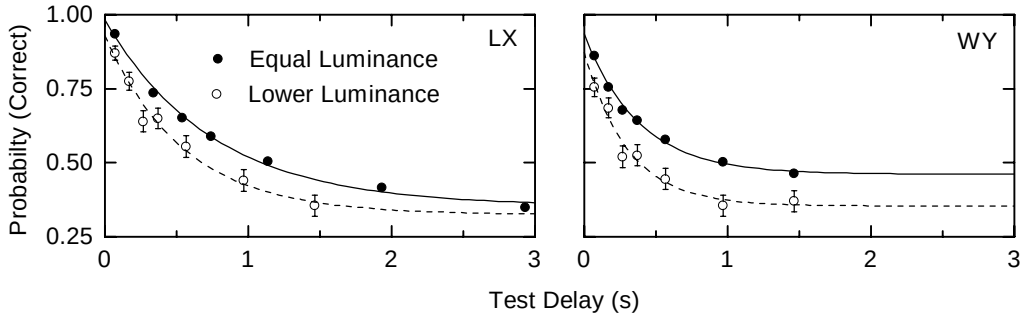

Figure 4.9. Effect of luminance decrease on partial-report performance in separate tests. The solid and dashed lines represent the best-fit exponential function for the equal-luminance and the lower-luminance stimuli respectively. Error bars represent the standard error for the values. The standard errors for the equal luminance data averaged over several test sessions are smaller than the symbol size.

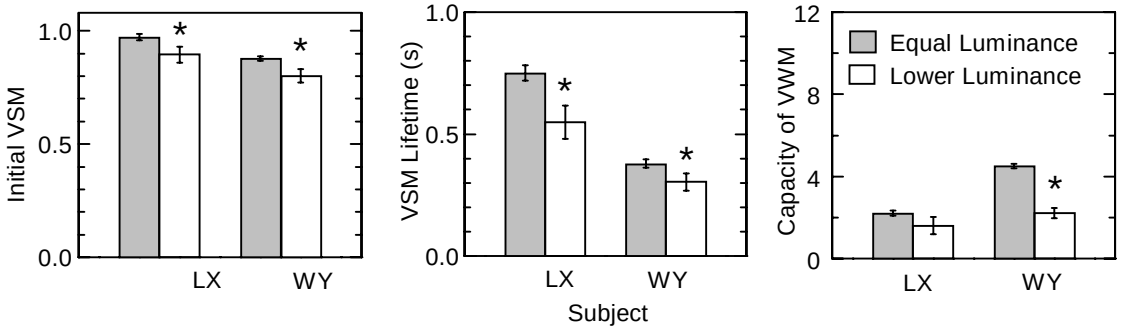

Figure 4.10. Effect of luminance decrease on initial level of visual sensory memory (P_i), lifetime of visual sensory memory (τ), and capacity of visual working memory (C_w). Stimuli of different luminance were tested in separate sessions. Error bars represent the standard error of the values.

A luminance decrease clearly produces a significant effect on partial-report performance for both subjects. The specific effect on VSM and VWM are presented in Figure 4.10 by contrasting the parameters for these memories in the two stimulus conditions for each subject. The parameters were deduced from the model introduced in section 2.1.

A decrement of the grating luminance below the background significantly decreased initial VSM level for both LX ($z = 1.70$, $p < 0.05$) and WY ($z = 2.53$, $p < 0.05$). This is similar to the effect of a luminance increase. Both manipulations enhance the power of the low spatial frequency components defining the global structure of the display, which is the large circle formed by the 12 grating patches. These similar effects suggest a competition between the different stimulus features composed of different spatial frequency components.

A luminance decrement also significantly decreases the VSM lifetime for both LX ($z = 2.63$, $p < 0.05$) and WY ($z = 1.79$, $p < 0.05$). The decrements of the lifetimes was 0.2 s for LX was and 0.08 s for WY, with the mean of 0.14 s, which was about half of the mean lifetime reduction of 0.31 s caused by a luminance increase for the same subjects in Experiment 7.

A luminance decrease has a significant inverse effect on the capacity of VWM for WY ($z = 8.81$, $p < 0.05$), but it was not significant for LX ($z = 1.39$, $0.10 > p > 0.05$).

In conclusion, the effect of a luminance decrement on the VSM was similar to that of luminance increment: It decreases its initial level and shortens it lifetime. The

results of this experiment confirm the prediction of the spatial-frequency channel hypothesis. However, this decrement effect was about half of that caused by the increasing the mean luminance of the isoluminant standard stimuli above that of the background. It seems that adaptation also plays a role in these experiments, partially canceling the effect caused by the spatial-frequency mechanism. These data suggest that both mechanisms jointly influence the VSM lifetime, but the spatial-frequency mechanism dominates in the specific experimental conditions of this study.

4.6 Experiment 9: Effect of Stimulus Contrast on VSM Lifetime: Separate Tests

This experiment examined the effect of a contrast change on VSM lifetime when stimuli of different contrast were tested in separate sessions.

4.6.1 Method

Subjects. Two of the four subjects of Experiment 2 volunteered as subjects for this experiment. All had normal or corrected-to-normal vision.

Procedure. The procedure was the same as the standard test (section 2.1) except that the mean luminance of the gratings was decreased by 6.5 cd/m^2.

4.6.2 Results and Conclusions

Partial-report performance for stimuli of high contrast are presented in Figure 4.11. Also presented in the figure are the data for the standard stimuli with lower contrast as presented in Figure 3.11.

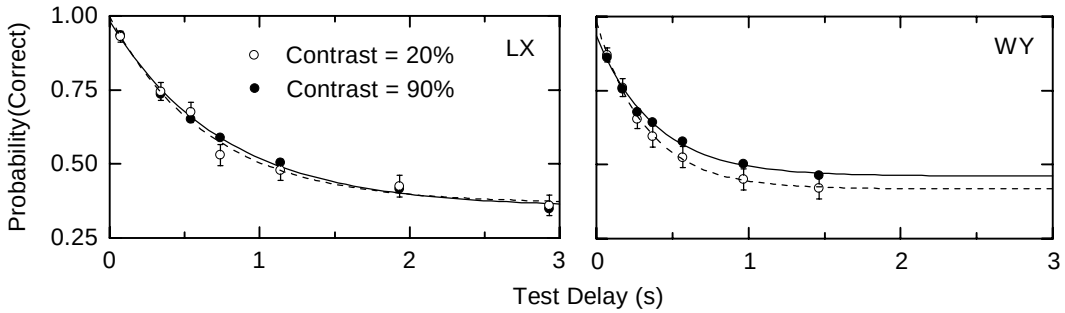

Figure 4.11. Effect of stimulus contrast on partial-report performance in separate tests. The solid and dashed lines represent the best-fit exponential function for the contrast of 20% and 90% respectively.

The effect of increasing the stimulus contrast has no influence on partial-report performance for LX [t (6) = 0.53, $p > 0.05$], but it decreases the overall performance significantly for subject WY [t (6) = 2.97, $p < 0.05$]. The effect specific to VSM and VWM are presented by contrasting the three parameters for these memories in the two experimental conditions for each subject in Figure 4.12. The parameters were deduced from the model introduced in section 2.1.

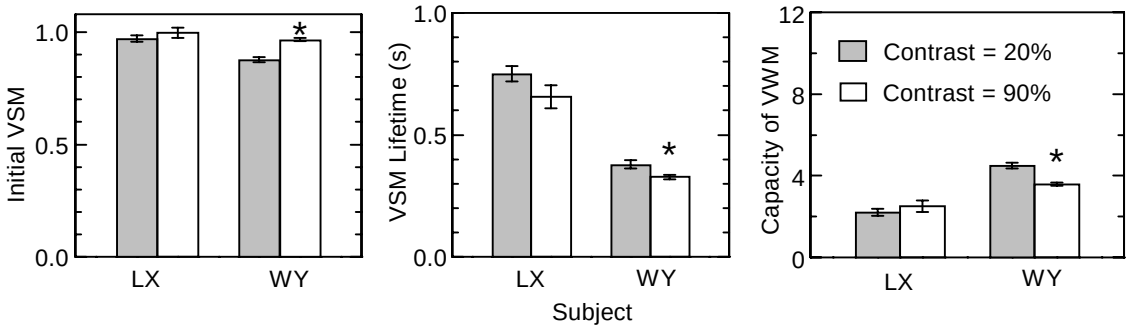

Figure 4.12. Effect of stimulus contrast on initial level of visual sensory memory (P_i), lifetime of visual sensory memory (τ), and capacity of visual working memory (C_w). Stimuli of different contrast were tested in separate sessions. Error bars represent the standard error of values.

Contrast effect on initial VSM. Enhancement of the stimulus contrast increases the initial VSM for both subjects: The enhancement was significant for WY ($z = -6.36$, $p < 0.05$) but not significant for LX ($z = -1.34$, $0.10 > p > 0.05$). The latter was probably due to the fact that the initial VSM level for the equal luminance stimuli was close to perfect so that there was no opportunity to improve. As shown in Experiment 1, WY had a lower initial VSM level than the other practiced subjects, and a detailed examination of the data suggests that he had difficulty in perceiving the items at locations corresponding to 7 and 11 o'clock. The significant improvement of the initial VSM level in this experiment indicates that his deficit in perceiving items at these two locations could be largely remedied by enhancing the stimulus contrast. This suggests that the difficult at these two locations was probably due to a higher contrast threshold.

Contrast effect on VSM lifetime. There was a consistent slight decrement of VSM lifetime for LX and WY. The effect was significant for WY($z = 2.24$, $p < 0.05$), but not for LX ($z = 1.54$, $0.10 > p > 0.05$).

Contrast effect on VWM. There was a consistent slight decrement effect on VWM by enhancing the stimulus contrast; the effect was significant for WY($z = 5.76$, $p < 0.05$), but not for LX ($z = -0.87$, $p > 0.10$).

In conclusion, the results of this study are consistent with those of Experiment 2 where the trials with high and low contrast stimuli were mixed in a test session: Further enhancement of the contrast of a clearly visible stimulus has no consistent effect on the two memories underlying the performance. Although a significant effect of increasing

the stimulus contrast on VSM lifetime was obtained only for WY in this experiment, the direction of this effect was the same for all the subjects in this experiment and Experiment 2. The decrement of the VSM lifetime caused by the contrast enhancement was about only 1/4 of that caused by luminance increment in Experiment 7. It should be noted that the change of contrast from 20% to 90% almost covered the range of the clearly visible patterns with a presentation duration of 28 ms, while the luminance change was about only 16% from the background. Thus, the critical variable for the inverse stimulus intensity effect is the change of overall luminance.

4.7 Conclusions

For the standard stimuli (Figure 2.1), an increase in presentation time from 28 ms to 200 ms does not affect VSM lifetime; increasing the contrast of gratings from 20% to 90% while maintaining its mean luminance the same as the background slightly reduces the VSM lifetime, but the effect was too small to be significant for each subject; a slight change in the mean luminance of the gratings above or below the background largely reduces the VSM lifetime for each subject. Such luminance effect might be due to the different temporal properties of the spatial frequency channels in the visual pathway.

CHAPTER 5. NEURAL SUBSTRATE OF VISUAL SENSORY MEMORY

This part of the study examines the neural basis for VSM by assessing the correspondence between its lifetime and the lifetimes of cortical activation traces established by the same visual pattern. Although a cortical source for VSM has been implied by some psychophysical studies (see Breitmeyer, 1984 for a review), no direct physiological evidence was provided, and the specific cortical area remained to be identified.

5.1 Current Studies of Memories in the Brain

Investigations of memory functions in the human brain have been focused on the changes in synapse efficacy (Bliss et al., 1993; Hawkins et al., 1993), and the early neural network models simulate memory functions by changes in synaptic strength (Churchland & Sejnowski, 1992). Recently, it was proposed that memory may well be represented by the intrinsic membrane properties of neurons (Marder et al.,1996). Thus, memory in networks may result from an ongoing interplay between changes in synaptic efficacy and intrinsic membrane properties.

Experimental studies of memory functions in the human cortex have primarily been based on relatively noninvasive brain imaging techniques like fMRI or PET. Due to the limited temporal resolution of these techniques, these memory function studies focus on the long-term explicit or implicit memories lasting from days to years (e.g., Squire & Knowlton, 1995) and short-term working memory lasting for seconds to tens of seconds (e.g., Desimone et al., 1995). Because of the highly transient nature of VSM neither

fMRI nor PET are appropriate tools. Crick and Koch (1990) have referred to iconic memory, the classic concept of VSM, as a "more transient awareness" or "fleeting awareness", and acknowledged that as"…this appears very difficult to study, we should say nothing more about it".

Crick and Koch (1990) suggested that iconic memory is a rapid synaptic modification which always involves the continued firing of relevant neurons, with the likely involvement of reverberatory circuits of neurons of some sort or another. Grossberg and Mingolla (1985) suggested that visible persistence may be due to the persistence of reverberating activation beyond stimulus offset, which is probably generated by excitatory feedback loops. Such ideas were further pursued to simulate visible persistence by Francis and his colleagues (Francis, 1996a; Francis, 1996b; Francis & Grossberg, 1996; Francis, Grossberg, & Mingolla, 1994).

5.2 Approaches to the Temporal Properties of Visual Cortical Activation

5.2.1 Temporal Tuning

The responsiveness or the sensitivity of visual cortical neurons as a function of the temporal frequency of sinusoidally modulated stimuli have been extensively investigated to characterize the visual system's response properties (e.g. De Valois et al., 1982; Hawken, Shapley, & Grosof, 1996; Lennie et al., 1990). The V1 cells that show band-pass temporal-frequency tuning have been suggested to be the neural substrate of the band-pass temporal frequency channels inferred from psychophysics.

However, the relationship between these temporal properties measured by temporal-frequency tuning and the time course of VSM has not been studied. It was noted by Graham (1981) that if the system under consideration is linear, or approximately linear, the time course of the persistence of the sensory response is revealed by the region exhibiting the low-temporal-frequency decline.

5.2.2 Persistence of Firing

It is a common observation that the firing of neurons following a brief stimulus can persist for short period beyond the stimulus offset. The relationship between the time course of firing persistence and visible persistence has been assessed by Duysens et al. (1985). They measured the firing rate of cortical cells in area 17 of the cat elicited by a stationary light bar flashed for different duration. They found that 13 out of 72 cells with non-overlapping On and Off subregions were able to respond to the briefest On stimulus (12.5 ms) for low and moderate contrasts. The responses of these cells outlasted the brief On stimuli, and this neural persistence increased as the On duration was shortened, mimicking the inverse duration effect of visible persistence.

5.2.3 Synchronization

Fries et al. (1997) proposed that the synchronicity of the firing rather than the amplitude of the firing rate in the primary visual cortex is correlated with visual perception. This conclusion was based on their observation that in visual area 17 of awake strabismic cats, dynamic selection and suppression of sensory signals are associated with modifications of the synchrony rather than the rate of neuronal

discharges. By contrast, only a small percentage of neurons in the primary visual cortex in the awake monkey change their rate of discharge as a function of the perceptual state in a rivalry situation (Leopold & Logothetis, 1996).

Synchronization in visual cortex has been proposed to serve as the mechanism for feature linking within separate regions of cortex (Gray et al., 1992; Singer & Gray, 1995). It is conceivable that the continued synchronization after stimulus termination supports the VSM function. The duration of the synchronized response lasts from 100 to 900 ms (Gray et al., 1992). Recent studies have shown that the synchronization in human visual cortex could be measured by EEG and MEG recordings (Ribary et al., 1991; Tallon-Baudry et al., 1997). However, the existence and the functional role of these oscillatory synchronization remain controversial (Ghose & Freeman, 1992; Tovee & Rolls, 1992; Young et al., 1992). Any correlation between VSM and synchronized activity in the visual cortex is has yet to be established.

5.2.4 Activation Traces Deduced from the Habituation of Evoked Responses

A noninvasive method to characterize cortical activation traces in human brain was developed by Lu et al. (1992) with the magnetic source imaging (MSI) technique, which reveals intracellular cortical currents of coherently active populations of cells in the cerebral cortex. They found that the amplitude of an auditory evoked response in the primary auditory cortex follows the function: $A(1-e^{-ISI/\tau})$, where ISI is the interstimulus interval, τ is the lifetime for the activation trace, and A is the maximum response amplitude achieved for very long ISIs. They assumed that the observed evoked response

is the amount of input needed to recharge the activation trace to its full strength. Thus, this habituation function is complementary to the decay of the activation trace.

Lu et al. (1992) found that the lifetime of the activation trace in the primary auditory cortex elicited by a brief auditory stimulus accurately predicted the lifetime of auditory sensory memory (*echoic memory*) determined psychophysically for each of four subjects. This result suggests that the activation traces in different cortical regions serve various memory functions.

With the same paradigm, Uusitalo, Williamson and Seppa (1997) characterized the diverse cortical activation traces established by responses to a brief visual stimulus. The lifetime for the activation trace in cortical area V1 was 0.19 ± 0.03 and 0.29 ± 0.05s for two subjects respectively, and the activation traces in functionally higher cortical areas exhibited progressively longer lifetimes, with the longest lifetimes attaining 19 s in frontal cortex and 24 s in the parietal-occipital region.

5.3 Primary Visual Cortex (V1) and VSM

The V1 lifetimes 0.19 ± 0.03 to 0.29 ± 0.05s for the two subjects in Uusitalo, Williamson and Seppa (1997) are comparable to the time course of VSM in the previous studies (e.g. Sperling, 1960) and the results of this study. The mean VSM lifetime for the naïve subjects in Experiment 1 and other pilot studies for their first test session was 0.17 s. This correspondence led to the hypothesis that the activation trace in V1 serves as the neural substrate for VSM.

In additional to a comparable time course, other similarities between V1 characteristics and that of VSM suggest that they are related. First, V1 is the first stage of cortical processing of visual information, which is prior to the stages of recognition and categorization. Second, it is the only cortical area that is free from the competition of multiple items for further processing because of its relatively small receptive field of about 0.2° (e.g., Boussaoud et al.,1991). It was found that when multiple items are presented within the receptive field of a cell (which could be accomplished in only V2 and V4), the cell's response is strongly influenced by which item is attended (Luck et al, 1997; Moran and Desimone, 1985). Thus, the small receptive field of V1 provides it with a large capacity to faithfully represent the detailed visual information which is necessary for vivid visual experience.

The next two experiments were to test the hypothesis that the activation trace in V1 is the neural mechanism for VSM. The strategy was to assess the correlation between the VSM lifetime and V1 lifetime.

5.4 Experiment 10: Individual Differences in V1 Lifetime

This experiment applied the habituation paradigm to VEP recordings to deduce the lifetime of the activation trace in V1 for the subjects whose VSM lifetimes were known. The correlation between the V1 lifetime and VSM lifetime in these subjects was assessed. A significant positive correlation would support the hypothesis that the activation trace in V1 serves VSM.

5.4.1 Method

Subjects. Subjects were those involved in Experiment 1. For subjects SH, HG, and KB, the V1 lifetime was measured right after the psychophysical test of their VSM lifetime in Experiment 1. For subject YS, the V1 lifetime was measured only after the intensive practice. For the other subjects had tested for VSM lifetime repeatedly, the V1 lifetimes were measured in a separate day with an interval of one to three days relative to the corresponding VSM lifetime measurement. To assess the intensive practice on V1 lifetime within a subject, a subject (JT) was recruited to repeatedly take the standard VSM test as described in section 2.1 and the V1 lifetime was measured at the early stage of practice and at the end of the intensive tests.

Apparatus and stimuli. The device for visual stimulation and the viewing conditions were the same as the standard VSM test described in section 2.1. Only one visual display was used for the habituation measurement, and it was the standard stimulus illustrated in Figure 2.1.

The VEP data acquisition system was assembled by the author with an amplifier (Grass, Model 12B-32), a Pentium-133 PC and an analog-to-digital (AD) board. The data acquisition and analysis were controlled by programs written by the author in a graphic programming language, LabView. The AD board and LabView are products of National Instrument (http://www.natinst.com/). The system was synchronized by sending a rectangular trigger signal of 5 ms duration from the stimulus presentation PC to the VEP data acquisition PC. The temporal resolution, amplification and synchronization of

the system were carefully calibrated before this experiment was conducted. The filter band-pass was set to be 0.01-100 Hz. The electrode positions were at O1, O, O2, with Cz as reference according to the 10-20 EEG system (Jasper, 1958).

Procedure. The stimulus presentation device and viewing condition were the same as the standard test (section 2.1). The subject pressed a key to start a stimulus presentation block where the stimulus was presented 210 times with a fixed interstimulus interval (ISI). The stimulus presentation duration was 28 ms, the same as for the standard test of VSM. The VEP recording started from the 10^{th} stimulus presentation in a block to record the stabilized VEP responses. The VEP for a given ISI was obtained by averaging the response for each stimulation after deleting responses that exhibited artifacts from the eye blinks. The percentage of trials deleted due to contamination of eye-blink varied across subjects and ISI conditions, with mean of 24% and standard deviation of 8%. The mean values and it ranged from 5% to 30% across subjects. After a block of recordings, the subject took a 3- minute break and then the next block was run with a different ISI. The order of the ISIs for the blocks was randomized.

5.4.2 Results and Conclusions

Lifetime of the activation trace in V1. For each subject, a component with latency about 140 ms in the VEPs was consistently observed and it exhibited the biggest amplitude at all three occipital locations. The latency of this component ranges from 130 to 150 ms across the subjects. The source of this component has been localized in V1 by recent MSI studies (Hatanaka et al., 1997; Uusitalo, Williamson and Seppa, 1997).

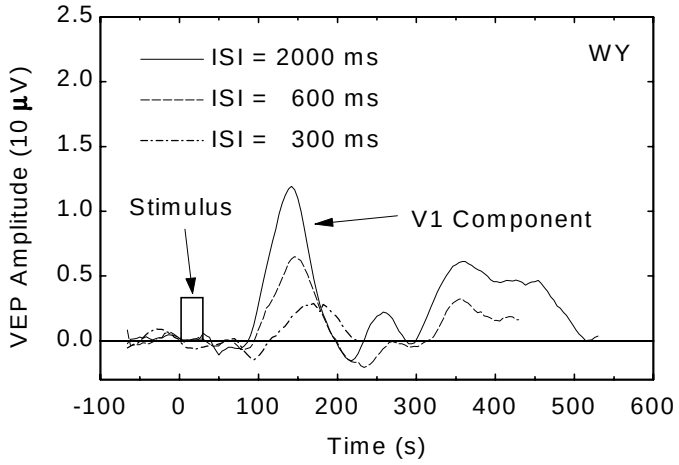

Figure 5.1. Visually evoked potentials (VEPs) for different ISIs in one representative subject. The lines represent the VEPs for three different ISI conditions. The VEPs presented here were recorded at the location O2 (reference Cz). Other two locations exhibited similar VEPs with smaller amplitude.

Figure 5.1 shows this V1 component in the VEPs of three different ISIs for one representative subject. Habituation of V1 response was evident in the decreasing of its amplitude as the ISI was decreased. Pilot studies found that the location exhibits the strongest V1 response varies across subjects, but its habituation characterized at these three occipital locations exhibit the same time constant. To achieve the best signal-to-noise ratio, the habituation of V1 response was characterized at the location exhibiting the strongest response for each subject. Figure 5.2 presents the habituation of the V1 response for each subject. Also presented are the best-fitting functions: $A - B\, e^{-ISI/\tau}$, where ISI is the interstimulus interval, τ is the time constant of the habituation, A and B characterize the response amplitude.

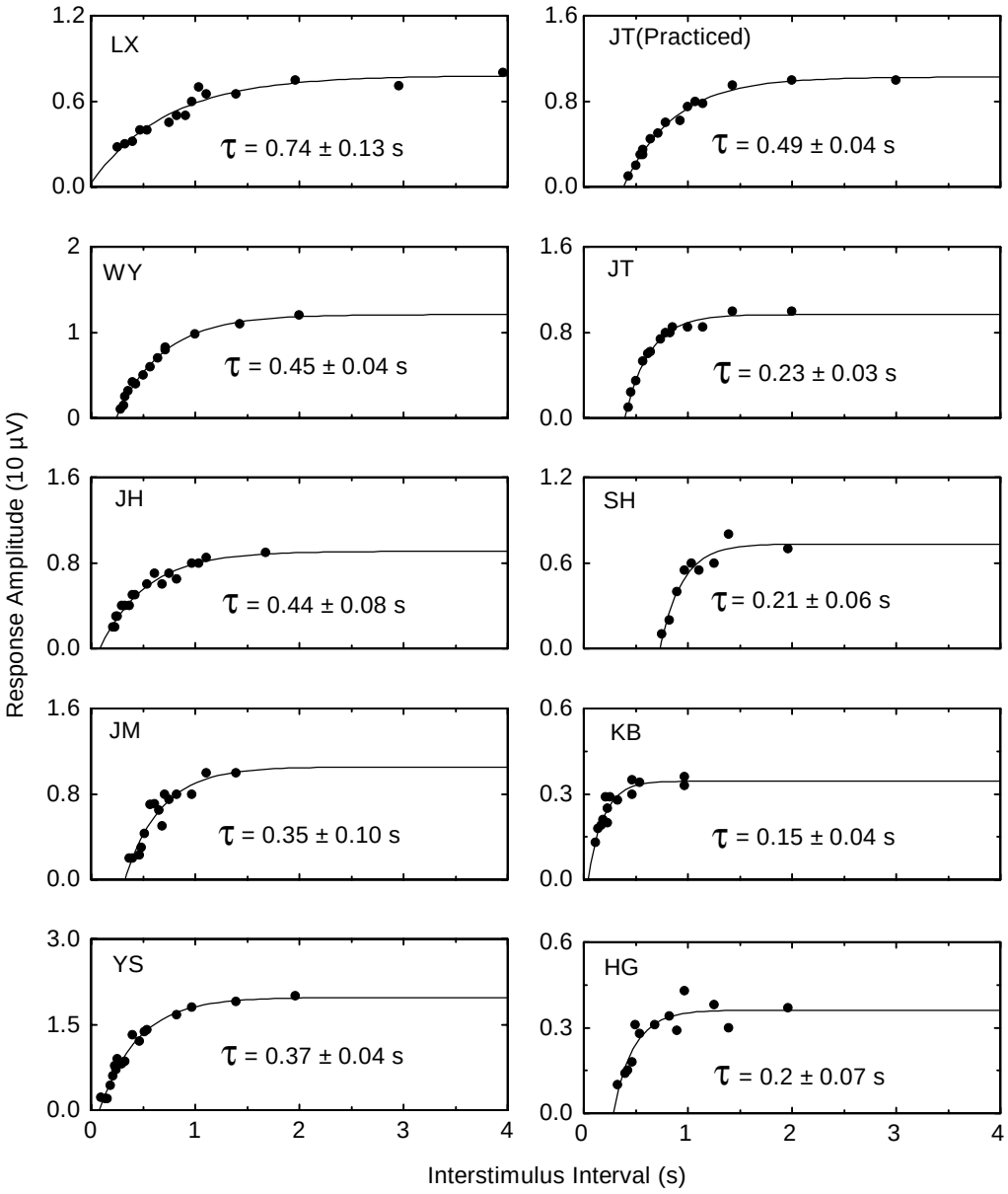

Figure 5.2. Habituation of the primary visual cortex (V1) response for each subject. The values for τ represent the 95% confidence interval for the time constant of the habituation function. For subject JT, the habituation of V1 was characterized right after the 2nd and 24th visual sensory memory (VSM) test respectively.

According to the activation trace model (Lu, Williamson and Kaufman, 1992), the time constant of the exponential function τ reveals the lifetime of the activation trace in V1.

Correspondence between the VSM lifetime and V1 lifetime. To illustrate the correspondence between the VSM lifetime and V1 lifetime, the VSM lifetime was plotted against V1 lifetime for each subject in figure 5.3.

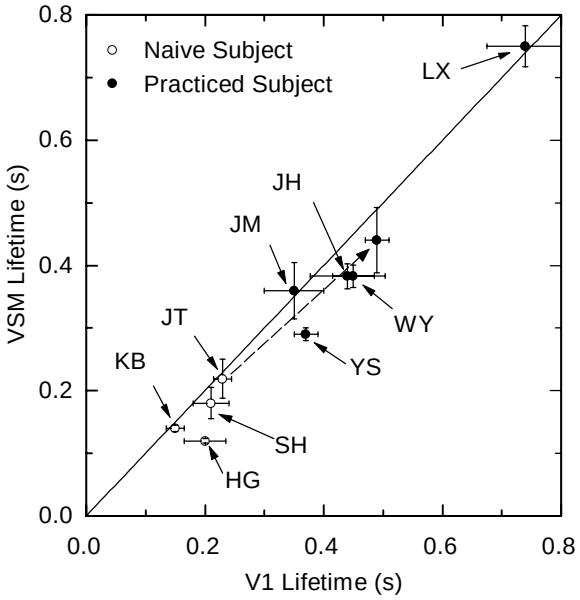

Figure 5.3. Correspondence between lifetime of visual sensory memory (VSM) and lifetime of the activation trace in the primary visual cortex (V1) for each subject. Subjects are indicated by their initials. Error bars represent the standard error of the lifetimes. The dashed arrow for JT indicates the enhancement of VSM lifetime by intensive practice.

The VSM lifetime assessed psychophysically was correlated [R (df = 9) = 0.98, p < 0.01] with the V1 lifetime measured physiologically. Furthermore, 96% of the variance was accounted for by the function $y = x$ which indicates that the lifetimes are precisely

matched for each individual. This result provides strong evidence supporting the hypothesis that the activation trace established by a brief visual stimulation underlies VSM.

The effect of intensive practice on VSM lifetimes in JT. Figure 5.3 presents the change of VSM lifetime with 30 repeated VSM tests for subject JT.

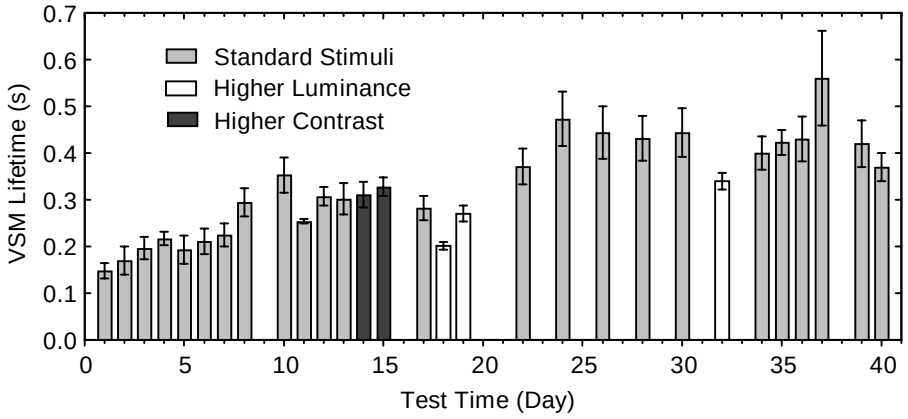

Figure 5.4. Enhancement of lifetime of visual sensory memory (VSM) by intensive practice for Subject JT. Error bars represent the standard error of the lifetimes. The higher-luminance stimuli were the same as those used in Exp. 7. The higher-contrast stimuli were the same as those used in Exp. 9.

The VSM lifetime was enhanced from the original level of 0.15 s to a ceiling level of about 0.45 s over 20 test sessions. Also presented in this figure were the VSM lifetime for the higher-luminance stimuli and the higher-contrast stimuli. Enhancing the contrast of the grating from 20% to 90% has no effect on the VSL lifetime. By contrast, increasing the mean luminance of the grating 6.5 cd/m^2 above the background decreases the VSM lifetime for JT. These results replicated the results of Experiment 7 & 9.

5.5 Experiment 11: Effect of Luminance Increase on V1 Lifetime

In Experiment 7, it was found that the VSM lifetime was reduced by about half by slightly enhancing the mean luminance of the gratings above the background. If the V1 activation trace serves VSM, its lifetime should also be shortened by this luminance increase. Experiment 11 assessed the effect of the luminance increase on the V1 lifetime.

5.5.1 Method

Subjects. Three of the practiced subjects in Experiment 1 volunteered to participate in this experiment.

Procedure. The procedure for assessing the V1 lifetime in this experiment was the same as in Experiment 10, except that the mean luminance of the gratings in the display was increased by 6.5 cd/m^2.

5.5.2 Results

The habituation functions of the V1 component of the VEP for the higher-luminance stimulus for each subject are presented in Figure 5.4. Also plotted in this figure are the habituation functions for the equal-luminance stimulus (Figure 2.1) for these subjects. Figure 5.5 compares these V1 lifetimes for the equal-luminance and higher- luminance stimulus for each subject.

Enhancing the mean luminance of the gratings above the background significantly shortens the V1 lifetime for LX ($z = 6.57$, $p < 0.05$), WY ($z = 3.6$, $p < 0.05$), and JH ($z = 5.58$, $p < 0.05$). The V1 lifetime was affected by the luminance change just as the VSM lifetime reported in Experiment 6.

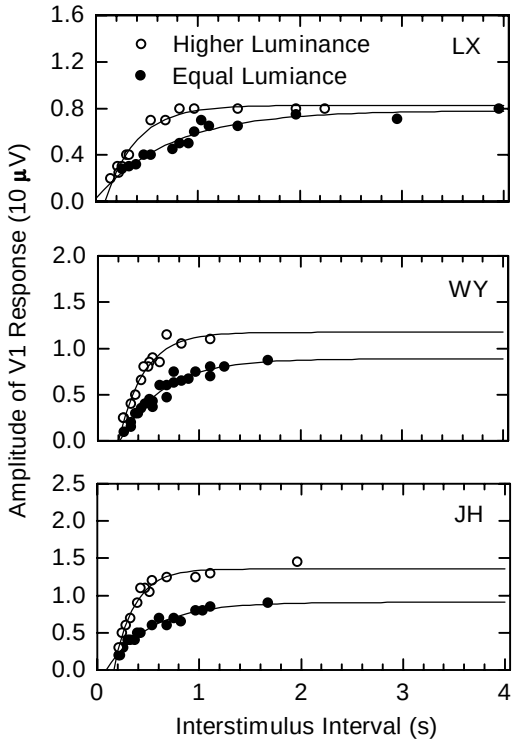

Figure 5.5. Effect of luminance increase on the habituation of primary visual cortex (V1) response.

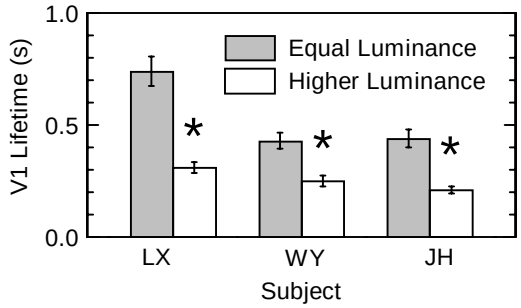

Figure 5.6. Effect of luminance increase on lifetime of the activation trace in primary visual cortex (V1). The error bars represent the standard error of the lifetimes.

To illustrate the parallel change of the VSM lifetime and V1 lifetime under the influence of luminance increase, Figure 5.6 presents the two lifetimes for each of the three subject in the two stimulus conditions.

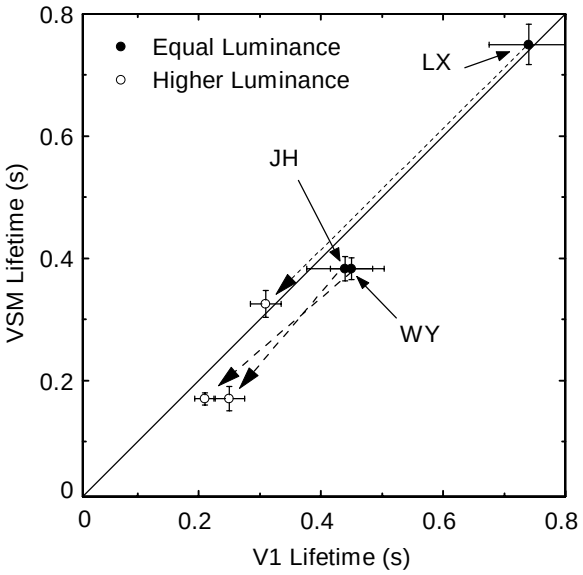

Figure 5.7. Parallel effects of luminance increase on lifetime of visual sensory memory (VSM) and lifetime of the activation trace in primary visual cortex (V1). Subjects are indicated by their initials. Solid and open circles represent lifetimes for equal-luminance and higher-luminance stimulus respectively. Error bars represent the standard error of the lifetimes.

This figure shows that the matched lifetimes for the equal-luminance stimulus still match when they were reduced by more than half by enhancing the mean luminance of the gratings above the background. Such a parallel change of these two lifetimes in each subject indicates that the two lifetimes are influenced by luminance increase in the same fashion. Thus, the VSM and V1 lifetimes are not just correlated across subjects, but also dynamically linked when they are modulated by changing stimulus parameters. This result further strengthens the hypothesis that the V1 activation trace underlies VSM.

5. 6 Conclusions

The lifetime of activation trace in V1 matches VSM lifetime in individual subjects over the range from 0.07 to 0.7 s. The psychophysical lifetime and physiological lifetime were equally enhanced by extensive practice for naïve subjects, and equally reduced by a luminance increase in stimuli. The close match of VSM lifetime and V1 lifetime provides strong evidence for the hypothesis that human VSM is represented at the cortical area V1.

CHAPTER 6. GENERAL CONCLUSIONS AND DISCUSSIONS

To achieve an accurate measurement for the time course of VSM in individual subjects, this study first reviewed previous studies of VSM in partial-report paradigm and identified the problems in this paradigm. Then the classic partial-report procedure (Sperling, 1960) was modified to efficiently characterize partial-report performance for individual subjects. A mathematical model was developed to isolate the VSM component underlying the performance. The results confirmed the exponential decay of VSM and its lifetime was defined.

The results of the experiments in chapters 3 & 4 indicate that the VSM lifetime of a subject could be prolonged by intensive practice and shortened by a change of the overall luminance in the stimuli. The enhancement effect of practice on VSM lifetime indicates that the VSM, which was thought of as a stimulus-driven sensory buffer, is not solely determined by the stimulus. It could be adapted by the task requirement to a certain level. Meanwhile, the shortening effect of luminance change on VSM lifetime suggests that the relative distribution of the spatial frequency components in the stimuli is the primary stimulus feature that determines VSM lifetime. Thus, the factors that influence VSM lifetime were identified. These results revealed the novel properties of VSM and provided good foundation for the identification of its neural substrate.

Experiments in chapter 5 found that the lifetime of the activation trace in V1 matches the VSM lifetime in each of the subject involved in this study. Such match even holds when the lifetimes were changed by the intensive practice and a luminance increase

in the stimuli for the subjects examined. Such strong correspondence between the lifetimes indicates that the activation trace in V1 is the cortical source for VSM.

The accurate measurement of the individual VSM lifetime revealed many novel properties of VSM in this study and thus provided a powerful tool to investigate the neural substrate of VSM. However, some questions regarding VSM still remain to be answered. For example, it is not clear whether the VSM characterized in this study is the subjective visible persistence. Although the inverse luminance effect observed favors the idea that VSM is the visible persistence, further effort is needed to directly assess their relationship.

The distribution of the spatial-frequency components in the stimuli was suggested as the primary factor that influences the VSM lifetime. It needs to be tested by directly by changing the distribution of the spatial-frequency components. In addition, the results of this study revealed a practice effect on the VSM lifetime. However, it is not clear whether the enhanced lifetime is specific to the tested stimulus feature, orientation of the gratings or is a characteristic of a coherent visual representation of the whole display. Further testing of the specificity of this practice effect will help to understand its underlying mechanism.

The mathematical model proposed in section 2.2 to isolate the VSM component underlying partial-report performance assumes that the VSM and VWM components contribute to partial-report performance independently. It is expected that these two memory components could be selectively influenced. For example, a concurrent VWM

task should reduce the number of items in the VWM in the partial-report task but leave the VSM lifetime unaffected. Such prediction should be tested in future studies.

The results of Experiments 11 & 12 provide strong evidence for the hypothesis that the activation trace in V1 serves VSM. However, it must be noted that the cortical activation trace is inferred from the habituation function based on the activation model. This activation trace is not directly observed and its neural mechanism is not clear at this moment.

The synchronized activity of neurons in the visual sensory cortex has been proposed as the neural mechanism for visual perception (Gray et al., 1992; Singer et al., 1995). The persistence of this activity in the primary visual cortex is a candidate for the neural mechanism of VSM, because VSM could be thought of as the persistence of perception beyond the real stimulus duration. A direct assessment of the correlation between these activities and VSM is difficult to attain because of the difficulties of applying the physiological measurements at the cellular level for human subjects. The 40 Hz component in the noninvasive VEP recordings for human subjects has been observed by Tallon-Baudry et al. (1997), but its functional role in visual perception and its relation to VSM is yet to be established.

The relation between the time course of habituation and that of memory is counterintuitive. The activation model (Lu, Williamson, & Kaufman, 1992) assumes that a component in VEP is what is needed to recharge the corresponding activation trace to its full strength. By this assumption, the reduction of the observed response shown as

habituation is caused by the residual activation trace at the time of responding. This suggests a dynamic gain-control mechanism in the sensory system. Such a mechanism is necessary to prevent saturation or overflow of the system, or to maintain a stable sensory representation under the normal viewing condition which involves small transient inputs due to microsaccades.

The relationship between the depression of a response and memory function has also been proposed in studies of the visual cortical area in the inferior temporal (IT) cortex (Miller & Desimone, 1994; Desimone, 1996). These researchers found that the response of 1/3 of the neurons in the perirhinal portion of IT cortex is reduced in amplitude when the same stimulus was repeatedly presented, and such a reduction in response could be maintained for minutes or a day (Fahy, Riches, & Brown, 1993). Desimone (1996) proposed that this repetition depression reveals a passive memory mechanisms for visual short-term memory.

Such habituation of the visual sensory response has also been extensively studied at the cellular level in the synaptic repetition-depression paradigm (Abbot et al, 1997; Markram & Tsodyks, 1996; Nelson, 1991a, 1991b; Tsodyks & Markram, 1997; Varela et al., 1997). The time constant of the repetition depression was found to be 150 – 900 ms which is about the same range as that of the habituation of the V1 response by VEP recordings in this study. The phenomenon of repetition depression was thought of as a form of cortical gain-control by depressing the postsynaptic responses to rapidly-firing afferents. Consequently, the postsynaptic cell can detect sudden rate changes in low- and

high frequency afferents with about equal sensitivity (Tsodyks & Markram 1997; Varela et al., 1997).

The synaptic repetition depression was found to be a presynaptic effect and was attributed to the depletion of the ready vesicle pool (Nelson, 1991; Tsodyks & Markram 1997; Varela et al., 1997). This suggests that the time constant of the exponential depression function reveals the time course of a passive recovery process. It was also proposed that such an activity-dependent synaptic depression might be caused by a postsynaptic activity via a negative feedback (O'Donovan & Rinzel, 1997). This idea is consistent with our observation of the strong correlation between the time constant of the habituation, or repetition depression of V1 response and the lifetime of VSM.

One possible mechanism for the dynamic link between the time course of the repetition depression in V1 and that of VSM could be that the activation trace that serves VSM sends a negative feedback to the presynaptic V1 relay and results in depressed postsynaptic response. To achieve the match between the time constant of the response depression in V1 and VSM lifetime, all that is needed is an assumption that the strength of the inhibitory feedback is proportional to the strength of the activation trace at any moment.

References

Anderson, R. B., & Tweney R. D. (1997). Artifactual power curves in forgetting. *Memory and Cognition*, **25,** 724-730

Abbot, L. F., Varela, J. A., Sen, K., & Nelson, S. B. (1997). Synaptic depression and cortical gain control, *Science*, **275**, 220-224.

Ahissar, M., & Hochstein, S. (1993). Attentional control of early perceptual learning. *Proc Natl Acad of Sci USA*, **90**, 5718-5722.

Allen, F. (1926). The persistence of vision. *American Journal of Physiological Optics*, **7**, 439-457.

Allport, D. A. (1989). Visual attention. In M. I. Posner (Ed.), *Foundations of Cognitive Science* (pp. 631-682). Cambridge, MA: MIT Press,.

Appelman, I. B. (1980). Partial report and other sampling procedures overestimate the duration of iconic memory, *American Journal of Psychology*, **93**, 79-97.

Atkinson, R., & Shiffrin, R. M. (1968). Human memory: A proposed system and its control processes. In K. W. Spence (Ed.), *Psychology of learning and motivation: Advances in research and theory* (vol. 2, pp. 89-195). New York: Academic Press.

Averbach, E., & Coriell, A. S. (1961). Short-term memory in vision. *Bell System Technical Journal*, **40**, 309-328.

Averbach, E., & Sperling, G. (1961). Short-term storage in vision. In C. Cherry (Ed.), *Symposium on information theory* (pp. 196-211). London: Butterworth.

Baddeley, A. (1998). Recent developments in working memory. *Current Opinion in Neurobiology,* **8**, 234-8.

Baddeley, A. D., & Hitch, G. (1974). Working Memory. In G. H. Bower (Ed.), *The Psychology of Learning and Motivation* (pp. 47-89). San Diego: Academic Press.

Bliss, T. V, & Collingridge, G. L., (1993). A synaptic model of memory: long-term potentiation in the hippocampus. *Nature,* **361**, 31-39.

Bourne, L. E., Dominowski, R. L., Loftus, E. F., & Healy, A. F. (1986). *Cognitive processes* (2nd ed.), Englewood Cloffs, NJ: Prentice-Hall.

Boussaoud, D., Desimone, R., & Ungerleider, L. G. (1991). Visual topography of area TEO in the macaque. *Journal of Comparative Neurology,* **306**, 554-75.

Boyton, R. M. (1972). Discrimination of homogeneous double pulses of light. In D. Jameson, & L. J. Hurvich (Eds.*), Handbook of sensory physiology: 4.Visual Psychophysics* (Vol. 7, pp. 202-232). New York: Springer.

Breitmeyer, B. G. (1984). *Visual masking: An integrative approach,* New York: Oxford.

Bors, D. A., & MacLeod, C. M. (1996). Individual differences in Memory. In E. L. Bjork, & R. A. Bjork (Eds.) *Memory* (pp. 412-436). Academic Press.

Brown, J. L. (1975). Afterimages. In C. H. Graham (Ed), *Vision and visual perception* (pp.479-503). John Wiley and Sons, New York.

Campbell, A. J., & Mewhort, D. J. K. (1980). On the familiarity effects in visual information processing. *Canadian Journal of Psychology*, **34**, 134-154.

Cavanagh, P. (1993). The perception of form and motion. *Current Opinion in Neurobiology,* **3**, 177-82.

Carrasco, M., & Frieder, K. S. (1997). Cortical magnification neutralizes the eccentricity effect in visual search. *Vision Research,* **37,** 63-82.

Chow, S. L., & Murdock, B. B., Jr. (1975). The effect of a subsidiary task on iconic memory. *Memory and Cognition,* **3**, 678-688.

Churchland, P. S., & Sejnowski, T. J. (1988). Perspectives on cognitive neuroscience. *Science,* **242**, 741-745.

Coltheart, M. (1972). Visual information processing. In P. C. Dodwell (Ed.), *New horizons in psychology*. Harmondsworth, England: Penguin Books.

Coltheart, M. (1977). Contemporary models of the cognitive processes. I: Information input and storage. In V. Hamilton, & M. D. Vernon (Eds.), *The development of cognitive processes*. London: Academic Press.

Coltheart, M. (1980). Iconic memory and visible persistence. *Perception & Psychophysics*, **27**, 183-228.

Coltheart, M., Lea, C. D., & Thompson, K. (1974). In defense of iconic memory. *Quarterly Journal of Experimental Psychology,* **26**, 633-641.

Cowan, N. (1995). *Attention and memory: an integrated framework,* Oxford University Press.

Crick, F., & Koch, C. (1990). Some reflections on visual awareness. *Cold Spring Harbor Symposia on Quantitative Biology,* **IV,** 953-962.

Desimone, R. (1996). Neural mechanisms for visual memory and their role in attention. *Proc Natl Acad Sci U S A,* **93**, 13494-13499.

Desimone, R., Miller, E. K., Chelazzi, L, & Lueschow, A. (1995). Multiple memory systems in the visual cortex. In Gazzaniga M. S. et al. (Eds.). *The Cognitive Neuroscience* (pp. 803-814). The MIT Press.

De Valois, R.L., Albrecht D. G., & Thorell L. G. (1982). Spatial frequency selectivity of cells in macaque visual cortex. *Vision Research,* **22**, 545-59.

Dick, A. O. (1967). Visual information processing and the memory trace. *Unpublished Ph.D. thesis,* University of Waterloo.

Dick, A. O. (1969). Relations between the sensory register and short-term storage in tachistoscopic recognition. *Journal of Experimental Psychology,* **82**, 279-284.

Dick, A. O. (1974). Iconic memory and its relation to perceptual processing and other memory mechanisms. *Perception and Psychophysics,* **16**, 575-596.

Di Lollo, V. (1978). On the spatial-temporal interactions of brief visual displays. In R. H. Day & G. V. Stanley (Eds), *Studies in Perception* (pp. 39-55), Perth: University of Western Australia Press.

Di Lollo, V. (1984). On the relationship between stimulus intensity and duration of visible persistence. *Journal of Experimental Psychology: Hum Percept Perform,* **10**, 144-51.

Di Lollo, V., & Dixon, P. (1988). Two forms of persistence in visual information

processing. *Journal of Experimental Psychology*: *Human Perception and Performance*, **14**, 671-681.

Di Lollo, V., & Dixon, P. (1992). Inverse duration effects in partial-report. *Journal of Experimental Psychology*: *Human Perception and Performance*, **18**, 1089-1100.

Dixon, P. (1985). Stimulus duration may affect partial-report performance. *Perception*, **14**, 63-66.

Dixon, P., & Di Lollo, V. (1991). Effects of display luminance, stimulus type, and probe duration on visible and schematic persistence. *Canadian Journal of Psychology*, **45**, 54-74.

Dixon, P., & Shedden, J.M. (1987). Conceptual and physical differences in the category effect. *Perception & Psychophysics*, **42**, 457-464.

Doost, R., & Turvey, M. T. (1971). Iconic memory and central processing capacity. *Perception & psychophysics*, **9**, 269-274.

Duncan, J. (1981). Directing attention in the visual field. *Perception & Psychophysics*, **30**, 90-93.

Duncan, J. (1983). Perceptual selection based on alphanumeric class: evidence from partial reports. *Perception & Psychophysics*, **33**, 533-547.

Duysens, J., Orban, G. A., Cremieux, J., & Maes, H. (1985). Visual cortical correlates of visible persistence. *Vision Research*, **25**, 171-178.

Eriksen, C. W., & Steffy, R. A. (1964). Short-term memory and retroactive interference in visual perception. *Journal of Experimental Psychology,* **68**, 423-434.

Fahy, F. L., Riches, I. P., & Brown, M., W. (1993). Neuronal activity related to visual recognition memory: long-term memory and the encoding of recency and familiarity information in the primate anterior and medial inferior temporal and rhinal cortex. *Experimental Brain Research,* **96**, 457-72.

Fisher, D. L. (1984). Central capacity limits in consistent mapping, visual search tasks: four channels or more? *Cognitive Psychology,* **16**, 449-484.

Francis, G. (1996). Cortical dynamics of lateral inhibition: visual persistence and ISI. *Perception & Psychophysics,* **58**, 1103-1109.

Francis, G (1996). Cortical dynamics of visual persistence and temporal integration. *Perception & Psychophysics,* **58**, 1203-1212.

Francis, G. & Grossberg, S. (1996). Cortical dynamics of boundary segmentation and reset: persistence, afterimages, and residual traces. *Perception,* **25**, 543-567.

Francis, G., Grossberg, S., & Mingolla, E. (1994). Cortical dynamics of feature binding and reset: control of visual persistence. *Vision Research,* **34**, 1089-1104.

Fries, P., Roelfsema, P. R., Engel, A. K., Konig, P., & Singer, W. (1997). Synchronization of oscillatory responses in visual cortex correlates with perception in interocular rivalry. *Proc. Natl. Acad. Sci.* **94**, 12699-12704.

Gegenfurtner, K. R., & Sperling, G. (1993). Information transfer in iconic memory experiments. *Journal of Experimental Psychology: Human Perception and Performance*, **19**, 845-866.

Ghose, G. M., & Freeman, R. D. (1992). Oscillatory discharge in the visual system: does it have a functional role? *Journal of Neurophysiology*, **68**, 1558-1574.

Graham, N. (1981). Psychophysics of spatial-frequency channels. In M. Kubovy, & J. R. Pomerantz (Eds.), *Perceptual Organization.* Lawrence Erlbaum Association

Gray, C. M., Engel, A. K., Konig, P., & Singer, W (1992). Synchronization of oscillatory neuronal response in cat striate cortex: temporal properties. *Visual Neuroscience*, **8,** 337-347.

Grossberg, S., & Mingolla, E. (1985). Neural dynamics of perceptual grouping: textures, boundaries, and emergent segmentations. *Perception and Psychophysics*, **38,** 141-171.

Haber, R. N. (1983). The impending demise of the icon: A critique of the concept of iconic storage in visual information processing. *Behavioral and brain sciences*, **6**, 1-54.

Haber, R. N. (1969). Information processing approaches to visual perception: An introduction. In R. N. Haber (Eds). *Information processing approaches to visual perception,* (pp. 1-15). Holt, Rinehart and Winston.

Hatanaka, K., Nakasato, N., Seki. K., Mizio, K., & Yoshimoto, T. (1997). Striate cortical generators of the N75, P100, and N145 components localized by pattern reversal

visual evoked magnetic fields. *Tohoku Journal of Experimental Medicine,* **182**, 9-14.

Hawken, M. J., Shapley, R. M., & Grosof, D. H. (1996). Temporal-frequency selectivity in monkey visual cortex. *Visual Neuroscience,* **13**, 477-492.

Hawkins, R. D, Kandel, E. R, & Siegelbaum, S. A. (1993). Learning to modulate transmitter release: themes and variations in synaptic plasticity. *Annual Review of Neuroscience,* **16**, 625-565.

Hawkins, H. L., & Shulman, G. L. (1979). Two definitions of persistence in visual perception. *Perception & Psychophysics,* **25**, 348-350.

Holding, D. H. (1970). Guessing behavior and the Sperling store. *Quarterly Journal of Experimental Psychology*, **22**, 248-256.

Holding, D. H. (1971). The amount seen in brief exposures. *Quarterly Journal of Experimental Psychology*, **23**, 72-81.

Holding, D. H. (1972). Brief visual memory for English and Arabic letters. *Psychonomic Science*, **28**, 241-242.

Holding, D. H. (1973). Recognition tests of visual information storage. *British Journal of Psychology,* **64**, 9-16.

Ishai, A., & Sagi, D. (1995). Common mechanisms of visual imagery and perception. *Science,* **268**, 1772-4.

Irwin, D. E., & Brown, J. S. (1987). Tests of a model of informational persistence. *Canadian Journal of Psychology,* **41**, 317-338.

Irwin, D. E., & Yeomans, J. M. (1986). Sensory registration and informational persistence. *Journal of Experimental Psychology: Human Perception and Performance,* **12**, 343-360.

Jasper, H. H. (1958). The ten-twenty electrode system of the international federation. *Electroencephalography and Clinical Neurophysiology*, **10**, 371-375.

Kahneman, D., Treisman, A., & Gibbs, B. J. (1992). The reviewing of object files: object-specific integration of information. *Cognitive Psychology,* **24**, 175-219.

Karni A, & Sagi D, (1993). The time course of learning a visual skill. *Nature,* **365,** 250-252.

Kaufman, L. (1974). *Sight and mind: an introduction to visual perception*. Oxford University Press.

Keele, S. W., & Chase, W. G. (1967). Short-term visual storage. *Perception & Psychophysics*, **2**, 383-386.

Kosslyn S.M., Thompson W.L., Kim I. J., & Alpert, N. M. (1995). Topographical representations of mental images in primary visual cortex, *Nature,* **378**, 496-8.

Landy, M. S., Cohen, Y. & Sperling, G. (1984). HIPS: A UNIX-based image processing system. *Computer Vision, Graphics, and Image Processing*, **25**, 331-347.

Lavie, N. (1995). Perceptual load as a necessary condition for selective attention. *Journal of Experimental Psychology: Human Perception and Performance,* **21**, 451-68.

Le Bihan, D., Turner, R., Zeffiro, T. A., Cuenod, C. A., Jezzard, P., & Bonnerot, V. (1993). Activation of human primary visual cortex during visual recall: a magnetic resonance imaging study, *Proc Natl Acad Sci U S A*, **90**, 11802-11805.

Legge, G. E. (1978). Space domain properties of a spatial frequency channel in human vision. *Vision Research,* **18**, 959-69.

Lennie, P., Krauskopf, J., & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience,* **10**, 649-669.

Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature,* **379**, 549-553.

Lindsay, P. H., & Norman, D. A. (1977). *Human Information Processing* (2nd. Ed.). New York: Academic Press, 1977.

Long, G. M., (1980). Iconic memory: A review and critique of the study of short-term visual storage. *Psychological Bulletin*, **88**, 785-820.

Long, G. M., (1982). Receptor interactions and visual persistence. *Vision Research*, **22**, 1285-1292.

Long, G. M., (1979). Comment on Hawkins and Shulman's Type I and Type II visual persistence. *Perception & Psychophysics***, 26**, 412-414.

Long, G. M., (1985). The variety of visual persistence: Comments on Yeomas and Irwin. *Perception & Psychophysics***, 38**, 381-385.

Long, G. M., & Beaton, R. J. (1982). The case for peripheral persistence: effects of target and background luminance on a partial-report task. *Journal of Experimental Psychology: Human Perception and Perform*, **8,** 383-391.

Lu, Z. -L., Williamson, S. J., & Kaufman, L. (1992). Physiological measures predict behavioral lifetime of human auditory sensory memory, *Science*, **258**, 1668-1670.

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology,* **77**, 24-42.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature,* **390**, 279-81.

Massaro, D. W., & Loftus, G. R. (1996). Sensory and perceptual storage: Data and theory. In E. L. Bjork & R. A. Bjork (Eds.) *Memory* (pp. 68-96). Academic Press.

Marder, E., Abbott, L. F., Turrigiano, G. G., Liu, Z., & Golowasch, J. (1996). Memory from the dynamics of intrinsic membrane currents. *Proc Natl Acad Sci U S A,* **93**, 13481-13486.

Markram, H., & Tsodyks, M (1996). Redistribution of synaptic efficiency between neocortical pyramidal neurons. *Nature,* **382,** 807-810.

Mayzner, M. S., Abrevayana, E. L., Frey, R. E., Kaufman, H. G., & Schoenberg, K. M. (1964). Short-term memory in vision: A partial replication of the Averbach and Coriell study. *Psychonomic Science*, **1**, 225-226.

Merikle, P. M. (1980). Selection from visual persistence by perceptual groups and category membership. *Journal of Experimental Psychology: General*, **109**, 279-295.

Mewhort, D. J., & Leppmann, K. P. (1985). Information persistence: testing spatial and identity information with a voice probe. *Psychological Research*, **47**, 51-58.

Mewhort, D. J. K., Campbell, A. J., Marchetti, F. M., & Cambpell, J. I. D. (1981). Identification, localization, and "iconic memory": An evaluation of the bar-probe task. *Memory & Cognition*, **9**, 50-67.

Miller, E. K., Desimone, R. (1994). Parallel neuronal mechanisms for short-term memory. *Science*, **263**, 520-2

Miller, E. K., Li, L., & Desimone, R. (1991). A neural mechanism for working and recognition memory in inferior temporal cortex. *Science*, **254,** 1377-1379.

Moates, D. R., & Schumacher, G. M. (1980). *An introduction to cognitive psychology*. Belmont, CA: Wadsworth.

Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, **229**, 782-784.

Mulligan, N. W. (1997). Attention and implicit memory tests: the effects of varying attentional load on conceptual priming. *Memory & Cognition*, **25**, 11-17.

Neisser, U. (1967). *Cognitive psychology*. New York: Appleton-Century-Crofts.

Nelson, S. B., (1991a). Temporal interactions in the cat visual system. I. Orientation-selective depression in the visual cortex. *The Journal of Neuroscience*, **11**, 344-356.

Nelson, S. B., (1991b). Temporal interactions in the cat visual system. III. Pharmacological studies of cortical depression suggest a presynaptic mechanism. *The Journal of Neuroscience*, **11,** 369-380.

Nisly, S. J., & Wasserman, G. S. (1989). Intensity dependence of perceived duration: data, theories, and neural integration. *Psychological Bulletin,* **106**, 483-96.

O'Donovan, M. J., & Rinzel, J.(1997). Synaptic Depression: a dynamic regulation of synaptic communication with varied functional roles. *Trends in Neuroscience***, 20**, 431-433.

Pashler, H. (1998). *The psychology of attention* (pp. 54-55). Cambridge, MA: MIT Press,

Pashler, H., & Carrier, M. (1996). Structure, process, and the flow of information. In E. L. Bjork, & R. A. Bjork (Eds.), *Memory* (pp. 3-29). Academic Press.

Phillips, W. A. (1974). One of the distinction between sensory storage and short-term visual memory. *Perception & Psychophysics*, **16**, 283-290.

Phillips, W. A. (1983). Short-term visual memory. *Philosophical Transaction to the Royal Society of London,* **B 302**, 295-309.

Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking multiple independent targets: evidence for a parallel tracking mechanism. *Spatial Vision,* **3**, 179-197.

Reed, A. V. (1976). The time course of recognition in human memory, *Memory & Cognition*, **4,** 16-30.

Ribary, U., Ioannides, A. A., Singh, K. D., Hasson, R., Bolton, J. P. R., Lado, F., Mogilner, A., & Linas, R. (1991). Magnetic field topography of coherent thalamocotical 40-Hz oscillations in humans. *Proceedings to the National Academical Science of USA*, **88,** 11037-11041.

Sagi, D., & Tanne, D. (1994). Perceptual learning: learning to see. *Current Opinion in Neurobiology*, **4**, 195-199.

Sakitt, B., & Appelman, J. B. (1978). The effects of memory load and the contrast of the rod signal on partial report superiority in a Sperling task. *Memory & Cognition*, **6**, 562-567.

Sakitt, B., & Long, G. M. (1978). Relative rod and cone contributions in iconic storage. *Perception & Psychophysics,* **23**, 527-536.

Sakitt, B., & Long, G. M. (1979). Spare the rod and spoil the icon. *Journal of Experimental Psychology: Human Perception and Performance,* **5**, 19-30.

Shapley, R., & Lennie, P. (1995). Spatial frequency analysis in the visual system. *Annual Review of Neuroscience*, **8**, 547-583.

Single, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience*, **18**, 555-586.

Squire, L. R., & Knowlton, J. (1995). Memory, hippocampus, and brain systems. In Gazzaniga M. S. et al. (Eds.). *The Cognitive Neuroscience* (pp. 803-814. The MIT Press.

Sperling, G. (1960). The information available in brief visual presentations**.**

Psychological Monographs, **74** (whole no. 498).

Sperling, G. (1963). A model for visual memory tasks. *Human Factors*, **5**, 19-31.

Sperling, G. (1967). Successive approximation to a model for short-term memory. *Acta Psychologica*, **27**, 285-293.

Sperling, G. (1970). Binocular vision: A physical and neural theory. *American Journal of Psychology*, **83**, 461-534.

Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Pernier, J. (1997*). The Journal of Neuroscience*, **17,** 722-734.

Townsend, V. M. (1973). Loss of spatial and identity information following a tachistoscopic exposure. *Journal of Experimental Psychology*, **98**, 113-118.

Tovee, M. J., & Rolls, E. T. (1992). The functional nature of neuronal oscillations [letter]. *Trends in Neuroscience*, **15**, 387-388.

Tsodyks, M., & Markram, H., (1997). The neural code between neocortical pyramidal neurons depends on neurotransmitter release probability, *Proceedings to the National Academic of Science of the USA*, **94**, 719-723.

Ungerleider, L. G., Courtney, S. M., & Haxby, J. V. (1998). A neural system for human visual working memory. *Proc Natl Acad Sci U S A*, **95**, 883-890.

Uusitalo, M. A., Williamson, S. J., & Seppa, M. T. (1996). Dynamic Organization of the human visual system revealed by lifetimes of activation traces. *Neuroscience Letters*, **213**, 149-152.

Varela, J. A., Sen, K., Gibson, J., Fost, J. Abbot, L. F., & Nelson, S. B. (1997). A quantitative description of short-term plasticity at excitatory synapses in layer 2/3 of rat primary visual cortex. *The Journal of Neuroscience*, **17**, 7926-7940.

Von Wright, J. M. (1972). On the problem of selection in iconic memory. *Scandinavia Journal of Psychology*, **13**, 159-171.

Walsh, V., Ashbridge, E., & Cowey, A. (1998). Cortical plasticity in perceptual learning demonstrated by transcranial magnetic stimulation. *Neuropsychologia*, **36**, 363-367.

Weichselgartner, E. & Sperling, G. (1985). Continuous Measurement of visible persistence. *Journal of Experimental Psychology: Human Perception and Performance*. **11,** 711-725.

Wolford, G, & Hollingsworth, S. (1974). Retinal location and string position as important variables in visual information processing. *Perception and Psychophysics*, **16**, 437-442.

Yantis, S. (1992). Multielement visual tracking: attention and perceptual organization. *Cognitive Psychology*, **24**, 295-340

Yeomans, J.M., & Irwin, D. E. (1985). Stimulus duration and partial-report performance. *Perception & Psychophysics*, **27**, 183-338.

Young, M. P., Tanaka, K., & Yamane, S. (1992). On oscillating neuronal responses in the visual cortex of the monkey. *Journal of Neurophysiology*, **67**, 1464-1474.